U.S. Department
of Commerce

Volume 104
Number 1
January 2006

Fishery Bulletin

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Periodicals postage is paid at Seattle, WA, and at additional mailing offices. POSTMASTER: Send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn.: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

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For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $55.00 domestic and $68.75 foreign. Cost per single issue: $28.00 domestic and $35.00 foreign. **See back for order form.**

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U.S. Department of Commerce
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Volume 104
Number 1
January 2006

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Precision and accuracy of fish length measurements obtained with two visual underwater methods

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Abstract—During the *VITAL* cruise in the Bay of Biscay in summer 2002, two devices for measuring the length of swimming fish were tested: 1) a mechanical crown that emitted a pair of parallel laser beams and that was mounted on the main camera and 2) an underwater auto-focus video camera. The precision and accuracy of these devices were compared and the various sources of measurement errors were estimated by repeatedly measuring fixed and mobile objects and live fish. It was found that fish mobility is the main source of error for these devices because they require that the objects to be measured are perpendicular to the field of vision. The best performance was obtained with the laser method where a video-replay of laser spots (projected on fish bodies) carrying real-time size information was used. The auto-focus system performed poorly because of a delay in obtaining focus and because of some technical problems.

Manuscript submitted 22 July 2003 to the Scientific Editor's Office.
Manuscript approved for publication 20 April 2005 by the Scientific Editor.
Fish. Bull. 104:1–9 (2006).

Visual sampling of marine systems by SCUBA divers and underwater vehicles is increasingly used to estimate animal abundances, to observe natural behavior and response behavior to fishing gear *in situ*, and to assess community interactions (e.g., Bublitz, 1996; Auster et al., 1997; Davis et al., 1997; Uiblein et al., 2002; Trenkel et al., 2004). Visual methods also allow estimates of population-size structures without the bias caused by the size selectivity of fishing gear. Visual techniques have been used in the wild for measuring the length of animals by SCUBA divers (e.g., Yoshihara, 1997; Pfister and Goulet, 1999; Harvey et al., 2002a) or by submersibles (Love et al., 2000; Yoklavich et al., 2000). They have also been employed for estimating the length frequency of the catch of live tuna to be fattened after capture (Harvey et al., 2003), and in aquaculture to estimate the size range of fish (Petrell et al., 1997). Until now these techniques were mainly used in shallow waters or tanks. Because of the optical characteristics of sea water—its turbidity, the variations in light intensity with depth and water movements and fish movements, these methods are subject to measurement errors. Estimating the order of magnitude of this measurement error has been the focus of many studies (van Rooij and Videler, 1996; Yoshihara, 1997; Harvey et al., 2001, 2002a, 2002b, 2003).

Efficient methods for measuring fish length *in situ* can also be used in deeper waters not accessible to divers. Parallel laser projected from a video camera onto the seafloor or fish bodies permit accurate measurements (Love et al., 2000; Yoklavich et al., 2000). Albert et al. (2003) measured fish lengths on a video screen and then transformed these measurements into real length knowing the distance of the camera from the ground, its tilt angle, and the horizontal opening angle of the camera. If fish are not on or close to the bottom, it is necessary to know their distance off the bottom to apply this method. Auster et al. (1997) and Norcross and Mueter (1999) measured fish size on a video screen when the fish appeared between the skids of their ROV. The screen measurement is then related to the known distance of the skids. This method relies on the fish and skids being in the same horizontal plane and on the fish being perpendicular to the axis of the camera. Krieger (1992) used a submersible to estimate the size of rockfish.

Two methods were tested during the *VITAL* cruise in the Bay of Biscay, in late August and early Septem-

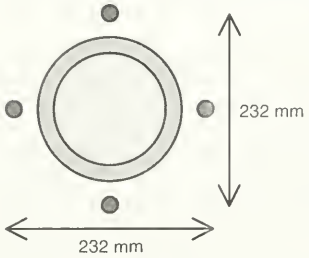

Figure 1

The four laser pointers mounted on a crown around the main camera in front of the ROV *Victor 6000*. The inner circle is the camera lens.

Figure 2

Laser spots (indicated by arrows) visible on and under a fish. These laser spots documented on videotape provided size information both in real time and during video replay.

ber 2002.[1] *Victor 6000*, a remotely operated vehicle (ROV) equipped with several video cameras and recorders, was operated at depths ranging from 1100 to 1500 m. Fish size was measured both by using a pair of parallel laser beams, and an auto-focus video camera linked to software for estimating object size based on the focal distance of the object in focus. In this study three sources of measurement variability were investigated: 1) systematic errors inherent to each method; 2) variability due to observer differences; 3) variability due to continuous fish movements and horizontal body orientation. To estimate these error components separately, rigid and articulated artificial objects ("artificial fish") of known size were measured repeatedly by several independent observers. Individuals belonging to several deep-sea fish species were also repeatedly measured. Mixed-effects models and heteroscedastic error models were fitted to the resulting measurements to compare the magnitude of errors due to different sources.

Materials and methods

Measurement devices

Both measurement devices were installed close to each other on the ROV *Victor*. The laser-beam crown was mounted on the main camera, which was itself attached to the pan and tilt unit. The METRAU© (SONY, model FCB-1X 47P) autofocus camera was mounted on the same pan and tilt unit.

Laser-beam pointers Four red laser pointers (10 mW, 635 nanometers [nm]) were mounted around the main camera housing (Fig. 1). The distance between each two opposite lasers was 232 mm. Red light is strongly attenuated by water but because of the relatively high power of the laser light-emitting diode (LED), a range of up to 7 m is reachable in clear waters.

To measure the fish and objects, the laser beams were projected on the target (Fig. 2). The laser spots, visible on the video, give size information both in real time and during video replay. The principle is simple, but several limitations exist. First, the measurement is correct only for an object located in a plane perpendicular to the laser axis. Second, the target should be large enough to be reached by at least two laser beams; the more laser impacts that are seen on the object to be measured, the easier the measurement.

For the measurement to be accurate, there must be a strict parallelism between the laser beams. This is complicated by the fact that the laser component itself (the diode with its optic lens) does not necessarily have a beam parallel to the axis of the component package. Further, designing an accurate alignment mechanism that is compatible with offshore and deep underwater operating conditions is difficult. The residual error after alignment is about 0.15°, which entails an error of 10 mm for the distance between two opposite spots at a distance of 4 meters (i.e., 4% of size).

METRAU camera The METRAU system is based on the autofocus video camera. The imaging device is an original equipment manufacturer (OEM) camera module similar to those used in off-the-shelf camcorders. The

[1] Trenkel, V. M., N. Bailly, O. Berthelé, O. Brosseau, R. Causse, F. de Corbière, O. Dugornay, A. Ferrant, J. D. M. ordon, D. Latrouite, D. Le Piver, B. Kergoat, P. Lorance, S. Mahévas, B. Mesnil, J.-C. Poulard, M.-J. Rochet, D. Tracey, J.-P. Vacherot, G. Veron, and H. Zibrowius. 2002. First results of a quantitative study of deep-sea fish on the continental slope of the Bay of Biscay: visual observations and trawling. ICES CM 2002/L:18, 2002, 15 p.

Figure 3
A METRAU video camera image with overlaid grid.

camera has a built-in automatic focus unit which adjusts lens settings to provide a sharp image. The camera is remotely controlled by a RS323 digital link and sends data back over this link, including zoom position and focal value (see details in Cadiou et al., 2004). A previous calibration in air and in a test tank provided correlation rules between raw data and field angle or focal distance.

When the system is operated, the data received by the computer are processed in real time. The object distance and the field angle are computed and a scale is overlaid on the video image (Fig. 3).

According to optical laws, the depth of focus decreases as the focal length increases. This means that in order to obtain an accurate measure of focal distance, a narrow field angle is required. In addition, the depth of focus increases when the focal distance moves towards infinity. Consequently, a domain of validity of the measurement can be defined. With the METRAU camera, there must be a target distance under three meters and a field angle of less than 6°. These constraints have to be combined with the following conditions: a steady image that would allow the automatic focal servo to stabilize; and avoidance of scenes with several image planes. In turbid waters, particles can create disturbing focal planes and affect the measurement process.

Measurement experiments

Artificial objects and live fish Objects of known size were used to estimate the potential bias in the length measurements obtained with the two devices. Three rigid objects—a can, a bottle, and a plastic tube measuring respectively 13, 30, and 66 cm—were repeatedly measured to evaluate device performance and observer-induced variability in the absence of errors induced by fish movement and variations in horizontal observation angles.

Fish movement makes the horizontal observation angle vary continuously. As a result, it is difficult to judge if and when an individual fish is perpendicular to the measurement axis. Further, fish seldom lie in a straight plane. Some species continuously flex their tail, others bend their whole body. To mimic the mobility of a real fish, a mobile object was built consisting of several pieces of Ertalyte (Quadrant Engineering Plastic Products, Bridgeport, CT) plates linked together with rope rings. This artificial fish was designed to be neutrally buoyant so that it could be moved by water currents and undulate like a real swimming fish. The "artificial fish" had three distinctively colored parts. Thus depending on how many parts were measured, a small (13 cm), medium (17 cm), or large (41 cm) "artificial fish" was the result. The real size of rigid objects and of the artificial fish was unknown to the observers throughout the measurement experiment.

In addition to measuring each of the rigid objects and the artificial fish, 351 individuals belonging to 21 deep-sea fish species were measured with both methods. The body sizes of these species ranged from 5 to 110 cm. Each individual fish was measured up to nine times. Altogether 2373 measurements were carried out.

Real time and postoperation measurements While the ROV was in operation, four to five observers were able to watch the video images. Real time measurements were performed by estimating sizes directly from the screen, without using any measuring instrument. Each observer was asked to write down his or her length estimate without announcing it, so that independent measurements were obtained. All artificial objects were measured by both trained and novice observers; real fish were measured only by trained observers, namely scientists and ROV pilots. All objects and fish were measured at distances of 2 to 5 meters.

Postoperation measurements were also performed on registered videos and digital images. For the laser method, the video tape was replayed. The tape was stopped when the image with an object or fish seemed to be in the best possible position. The fish or object was then measured with a ruler on the still video image. Postoperation measurements made with a ruler were also performed on digital snapshots taken from the videos in real time for both the laser and the METRAU method. A ruler was used rather than computer image analysis because it was easy and cost-efficient and it was felt appropriate for this trial appraisal of measurement methods. The bias introduced by this method was assumed to be negligible compared to observer-induced and fish-movement-induced errors.

Operational constraints prevented a full factorial design where all observers could use all methods and measure all objects.

Data analysis

Variance components for observers and fish movements The measurement variability due to observer differences

and fish movements was estimated from the measurements of the artificial objects, for which the true size was known. Because the measurement variance was expected to be larger for the mobile artificial fish than for the rigid objects, an extended linear mixed-effects model (Pinheiro and Bates, 2000) was used to account for this expected heteroscedasticity. The model included true length as a fixed effect and observer as a random effect. Fixed objects and mobile objects (artificial fish) were allowed separate variances. The resulting model was

$$L_{i,j} = \mu + \beta L^* + o_i + f_j + \varepsilon_{ij}, \quad (1)$$

where $L_{i,j}$ = length measured by observer i of an object of class j={fixed, mobile} and of true size L^*;
$o_i \sim N(0,\sigma(o))$; and
$\varepsilon_{ij} \sim N(0,\sigma)$, whereas $f_j \sim N(0, \sigma_j(f_i))$.

The model was fitted to the data from the eight observers who had measured all objects with the laser method.

Accuracy and precision for artificial objects An extended linear model including heteroscedastic variance terms was used to compare the precision and accuracy of the two methods. The model included fixed effects for true length and the measurement method. The estimated fixed effects allow assessment of the potential measurement bias of each method. The measurement errors for fixed and mobile artificial objects were modeled separately for each method. This allowed us to compare the precision of the methods. Thus, the fitted model was

$$L_{j,k} = \mu_k + \beta L^* + f_{jk} + \varepsilon_{jk}, \quad (2)$$

where k = the measurement method and j the object class as before. As in model 1, $\varepsilon_{jk} \sim N(0, \sigma)$. In contrast, $f_{jk} \sim N(0, \sigma_{jk}(f_{jk}))$ allowed for separate variances for each object-type and method pair. Only two trained observers used both measurement methods for all objects. Because there was no significant difference between their measurements, and in order to reduce the number of parameters to be estimated, no observer effect was included in this model.

Precision of fish measurements The precision of fish-length estimates was compared for two species, *Bathypterois dubius* and *Lepidion eques*. These species were selected for this analysis because they are abundant and relatively easy to measure, compared to other species that move faster or flex their body more often. Twenty-four individuals belonging to these two species were measured repeatedly by up to five observers using the real-time laser measurement method.

Because true fish size was unknown, measurement accuracy could not be estimated. For estimating the precision of fish measurements, an extended linear model with heteroscedastic errors was fitted to the fish length measurements. The model included a fixed individual fish effect (each fish had a different, unknown size) and a random observer effect; and fish species were allowed heteroscedastic variances to account for species behavior differences (*Lepidion* versus *Bathypterois*). The stationary species, *B. dubius,* is easier to measure compared to the more lively *L. eques*. The model was

$$L_{n,i,l} = \mu_n + o_i + s_l + \varepsilon_{nil}, \quad (3)$$

where $L_{n,i,l}$ = the length measurement obtained by observer i for individual fish n belonging to species l;
$o_i \sim N(0, \sigma(o))$; and
$\varepsilon_{nil} \sim N(0, \sigma)$, whereas $s_l \sim N(0, \sigma_l(s_l))$.

Unfortunately, it was not possible to carry out a direct comparison between the precision of size estimates of fish and artificial objects because the latter were measured seven to 11 times, whereas the former were measured only two to seven times. Random subsamples could be carried out to obtain comparable sample size; unfortunately, subsamples from large samples would still have a larger variance than small samples.

All models were fitted by using Splus 6.0 for Unix (MathSoft, Seattle, WA). For heteroscedastic models, because of identifiability constraints, the fitting algorithm provided estimates of the ratio between the standard deviations of each class in relation to the standard deviation of a specified class instead of the full set of standard deviations.

Results

Precision and accuracy of measurements varied among objects and methods (Table 1). The best precision was obtained with the video-replays of laser measurements, whereas METRAU generally did not perform very well, especially on snapshots. The precision was generally much lower for mobile objects than for rigid objects. Measurement bias was generally low for the laser method, whereas the METRAU method systematically underestimated the size of objects. A variety of fish species with various sizes were measured. CVs for individual fish measurements varied from 3% to 23% (Table 2). Species were grouped according to their motion behavior (1=sitting on bottom motionless, 2=station holding or drifting, 3=slow swimming, 4=fast swimming [Lorance and Trenkel[2]]). CVs were found to differ between groups, increasing with mobility (mean CV in group 1: 8.9%; group 2: 9.7%; group 3: 12.9%; group 4 was excluded because there was only one individual, $P<10^{-5}$).

[2] Lorance, P., and V. Trenkel. In preparation. Natural behaviour and reaction to an approaching ROV of large mid-slope species. IFREMER, Centre do Brest, B.P. 70, 29280 Plouzané, France.

Table 1

Summary of length measurements for artificial objects by five visual methods. Lengths (in cm) are given along with their coefficient of variation (%) and number of observations in parentheses. a.f. = artificial fish. The laser method entailed viewing laser points (that permit accurate length data) projected on fish. The METRAU method is based on an autofocus video camera.

Object	True size	Laser	Laser + video	Laser + snapshot	METRAU	METRAU + snapshot
Can	13	14.31 (13%, 26)	13.76 (3%, 5)	13.55 (4%, 5)	11.25 (7%, 10)	10.96 (7%, 5)
Bottle	30	30.87 (7%, 26)	31.90 (2%, 5)	31.47 (2%, 5)	26.90 (18%, 10)	32.05 (41%, 5)
Tube	66	65.62 (9%, 26)	66.40 (2%, 5)	66.66 (1%, 5)	44.25 (14%, 8)	40.75 (25%, 4)
Short a.f.	13	13.30 (13%, 21)	13.32 (6%, 3)	22.10 (23%, 2)	11.50 (6%, 2)	7.55 (33%, 6)
Medium a.f.	17	16.49 (14%, 21)	17.11 (5%, 3)	24.86 (25%, 2)	11.50 (18%, 2)	9.25 (32%, 6)
Large a.f.	41	40.80 (17%, 21)	44.87 (14%, 3)	63.23 (25%, 2)	30.00 (14%, 4)	23.21 (31%, 6)

Table 2

Summary of fish length measurements. n = number of individual fish measured for each species. m = total number of measurements. m/n = mean number of observations per individual. Mean length = average individual fish length (cm) per species. Mean CV = average individual coefficient of variation per species. Group = behavioral group of the species (1=sitting on bottom motionless, 2=station holding or drifting, 3=slow swimming, 4=fast swimming).

Species	n	m	m/n	Mean length	Mean CV	Group
Alepocephalus bairdi	2	4	2.0	48.4	8.2%	2
Bathypterois	87	586	6.7	19.2	8.9%	1
Breviraja caerulea	3	13	4.3	29.6	4.8%	2
Caelorinchus labiatus	15	73	4.9	28.7	10.2%	2
Cataetyx latyceps	1	5	5.0	24.1	12.4%	2
Chimaera monstrosa	6	23	3.8	91.4	9.2%	3
Coelorhyncus labiatus	2	8	4.0	25.4	14.9%	2
Coryphaenoides rupestris	21	77	3.7	45.4	12.1%	2
Cottunculus thomsoni	2	17	8.5	29.1	16.1%	1
Galeus melastomus	1	4	4.0	30.7	2.8%	4
Haplostethus atlanticus	6	27	4.5	32.6	9.4%	2
Hydrolagus affinis	1	6	6.0	74.9	23.3%	3
Hydrolagus mirabilis	3	6	2.0	78.4	11.9%	3
Lepidion eques	161	814	5.1	26.6	9.6%	2
Mora moro	3	8	2.7	60.0	7.9%	2
Nezumia aequalis	10	22	2.2	32.8	8.9%	2
Notacanthus	2	5	2.5	44.6	10.6%	2
Phycis blenoides	1	4	4.0	44.8	15.3%	2
Syphobranchus kaupii	7	23	3.3	27.2	16.2%	3
Trachyrincus murrayi	4	7	1.8	38.9	3.5%	2
Trachyscorpia cristulata echinata	14	67	4.8	40.7	8.1%	1

Measurement variance for observers and fish movements

The standard deviation of the observer random effect, $\sigma(o)$, amounted to approximately 20% of the residual standard deviation. The standard deviation of the random effect for mobile objects, $\sigma_{mobile}(f_{mobile})$, was 40% higher than that for rigid objects, indicating that the measurement variability was lower for fixed than for mobile objects, as expected. The slope and intercept of the fixed effects did not significantly differ from 1 and 0, respectively. Thus the laser method is unbiased and performs equally well for all sizes in the range tested (Table 3).

Accuracy and precision of measurements for artificial objects

Size measurements carried out using the laser beams in real time or on registered videos were found to be

Table 3

Estimated fixed-effect coefficients and standard deviations for model 1 for the measurements of rigid and mobile objects by eight independent observers using the laser method. SE = standard error; CL = confidence limit.

Coefficient	Estimate	SE	*P*-value
μ	1.53	0.97	0.12
β	0.976	0.023	<0.0001
Standard deviation	Lower CL	Estimated	Upper CL
$\sigma(o)$	0.296	1.126	4.435
σ	4.369	5.535	7.014
$\sigma_{rigid}(f_{rigid})/\sigma_{mobile}(f_{mobile})^1$	0.523	0.710	0.964

[1] Standard deviations were estimated in relation to the standard deviation for mobile objects.

Table 4

Estimated coefficients for model 2 for measurements of rigid and mobile objects by five variants of the two methods.

Coefficient	Estimate	SE	*P*-value
μ_{laser}	0.106	0.934	0.91
μ_{METRAU}	−7.198	1.621	<0.0001
$\mu_{laser+video}$	1.466	0.937	0.15
$\mu_{laser+snapshot}$	1.348	0.932	0.19
$\mu_{METRAU+snapshot}$	−9.516	1.806	<0.0001
β	0.976	0.023	<0.0001
σ	4.592		

Table 5

Estimates of the standard deviations of length measurements for rigid and mobile objects obtained by five variants of the two methods, from model 2. Number of measurements are given in parentheses. Estimates significantly different from 1 are in bold font.

Method	Rigid objects	Mobile objects
Laser	1.12 (21)	1.00[1] (9)
Laser + video	**0.21** (15)	1.03 (9)
Laser + snapshot	**0.19** (15)	3.43 (6)
METRAU	2.11 (20)	1.06 (8)
METRAU + snapshot	3.16 (14)	1.58 (18)

[1] All standard deviations are relative to the standard deviation for laser measurements of mobile objects.

unbiased, whereas the METRAU-based measurements underestimated the true length of objects by as much as 7 cm for real-time measurements and 10 cm for time-delayed measurements (Table 4, Fig. 4). In addition, the variance of METRAU measurements was systematically larger than the corresponding laser measurements (Table 5: ratios larger than 1). For rigid objects, laser-based video-replays had a lower variance than real time measurements. This lower variance for postoperational measurements was due to the allowance of videos to be replayed as many times as necessary in order to select the best image where an object was perpendicular to the optical axis. Use of a ruler also improves the measurement. The high estimation variance obtained for mobile objects measured with the laser method on digital snapshots was partially due to one outlier (Fig. 4B). The object was measured at a relatively great distance in somewhat turbid water. The outlier was not removed because these kinds of errors are to be expected under common measurement conditions in the field. Generally the most precise results were obtained for video-replays with the laser beam method.

Precision of fish measurements

The variance of the random effect for *B. dubius* was about 66% of the variance estimated for *L. eques*. For live fish, the standard deviation of the observer random effect was approximately 16% of the residual standard deviation (Table 6). This standard deviation is lower than that obtained for objects of known size because the residual variance was larger owing to the small number of repeated measurements obtained for each fish. It was not easy to repeatedly measure fish because of escapement behavior. In addition, only trained observers took part in this experiment, which reduced observer variability.

Discussion

The potential sources of errors and variability in visual fish length measurements are 1) the design and calibra-

Table 6

Estimates and 95% confidence limits for the standard deviations of the components of model 3 for fish size measurements obtained for two species by five independent observers using the laser method.

Standard deviation	Lower	Estimate	Upper
$\sigma(o)$	0.068	0.278	1.130
σ	1.096	1.702	2.642
$\sigma_{B\ dubius}(S_{B\ dubius})/\sigma_{L.eques}(S_{L.eques})^1$	0.41	0.66	1.06

[1] Standard deviations provided in relation to the standard deviation for *Lepidion* measurements.

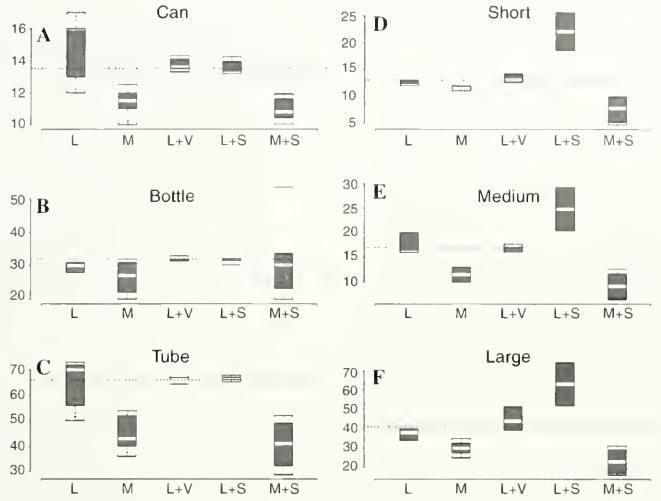

Figure 4

Boxplots for the distributions of length measurements (cm) obtained by five measurement methods for each of three fixed (left) and three mobile (right) objects. Boxes = interquartile range, white line = median, whiskers = extremes (excluding outliers). Dotted line is the true size of the object. L = laser method; M = METRAU method; L+V = laser video-replay; L+S = laser snapshot measurement; M+S = METRAU snapshot measurement.

tion of the measurement devices, 2) differences among observers, 3) orientation and position of fish in relation to the camera, and 4) swimming motion. We investigated each of these featuress.

Among the two methods tested during this study, the METRAU method performed poorly. It has several disadvantages. First, METRAU system needs the fish brought into focus when it is perpendicular to the field of vision. This may take time during which the fish can escape. Second, the registered video images do not include the superimposed calculated scales. Thus, unlike the laser method, it is not possible to replay the video to identify the best image. Postoperational measurements can be performed only by using the digital snapshots registered in real time. Third, this method had a higher variance than the laser method, probably because of the technical constraints just mentioned. Fourth, during the *VITAL* cruise the estimates were systematically biased downwards. Measurements carried out after the cruise in a laboratory pool confirmed this systematic underestimation to be ~20% of the real sizes. This result may be due to errors in the software which processes the output of the camera. Although the errors could probably be fixed, and the hardware improved to generate a video signal with the overlaid scale for recording, the other disadvantages are more difficult to eliminate, because of the intrinsic limitations of the system. Hence the method is not promising for estimating the size of fish in the wild.

By contrast, the laser beam method performed rather well, at least for rigid objects. We obtained CVs of 7–13% for rigid objects in real time and 1–4% with image postprocessing (Table 1), both of which compare well with CVs for silhouette measurements obtained with a single camera placed in a laboratory pool (with scale bars placed on the bottom of the pool) and with computer image processing (1%, Harvey et al., 2002b), or even with stereo-video measurements of silhouettes (0.6–7.5%, Harvey and Shortis, 1996). Length measurements were always unbiased and postoperational measurements on video images reached a high precision for rigid objects and for small- to medium-size mobile objects. Thus the method seems suited for measuring the size of animals of low mobility, like invertebrates, along visual observation transects.

The variance due to differences between observers was about 20% of the residual variance. This variance was reduced to 16% when measurements were performed by trained observers. This is true for real-time measurements. For video-replays of the laser-beam data, the variance due to observers was very small because of the use of a ruler instead of subjective extrapolation of

the known laser distance. The use of automated analysis of video images may further reduce the observer error source.

The major difficulty in measuring fish length *in situ* is caused by fish mobility, which causes them to be in variable orientations and positions in relation to the camera, and also to be flexed. We addressed both variance components together by comparing measurements of mobile objects ("artificial fish") and rigid objects. With the laser beam method, the measurement standard deviation of rigid objects was estimated to be 20% of the standard deviation of mobile objects (95% confidence limits: 6–75%). These components may be of the same order of magnitude as those for fish measurements, although fish measurements could not be estimated in our study because the true size of the fish was unknown. An attempt to disentangle both components is provided by estimating the difference between the precision obtained for species with contrasting behaviors. *Bathypterois dubius* individuals lie motionless on the bottom and seldom move, but because they stand on their fins they are never exactly perpendicular to the camera. By contrast, *L. eques* swims close to the bottom and tends to escape when the ROV is approaching too closely. This species continuously moves its tail; therefore it is very difficult to obtain an image with the whole body properly orientated and straight. The standard deviation of *B. dubius* length measurements was estimated to be 66% of that of *L. eques*. This difference is smaller than the difference between rigid and mobile objects above; therefore we conclude that the major part of variance is due to the orientation of the fish in relation to the camera. Similarly, the estimated CVs of 21 species grouped by motion behavior differed only slightly. This is consistent with previous studies which have shown that relative errors of single-camera or stereo-video measurements of silhouettes or frozen fish could reach 10% to 30%, depending on the distance to the camera, when the angle to the camera was increased from 0° to 60°, whereas the measurement CVs increased fourfold (Harvey and Shortis, 1996; Petrell et al., 1997; Harvey et al., 2002b). By contrast, error due to tail flexion and muscle contractions during swimming motions was estimated at ~5% in a comparison of "linear" to "sinusoidal" length of dorsally photographed sharks (Klimley and Brown, 1983) and at 0.5% for repeated stereo-video measurements of swimming tunas (Harvey et al., 2003).

In conclusion, the major source of measurement error for live fish may be their orientation and position in relation to the camera. For animals that are sessile or lying immobile on the ocean floor, this would be much reduced if the camera and laser beams were mounted vertically instead of obliquely. Thus the laser-beam method may be potentially useful for measuring benthic animals. For mobile animals, however, stereo-video methods (Harvey et al., 2001; Harvey et al., 2002a; van Rooij and Videler, 1996) may be more promising, and are continuously improving (Harvey et al., 2003).

Acknowledgments

We thank all observers for taking part in the experiment, and the ROV pilots for their willingness and skill at pursuing fish and in obtaining positions suitable for being measured. An anonymous referee gave very helpful comments on a previous version of this manuscript.

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The effect of predation (current and historical) by humpback whales (*Megaptera novaeangliae*) on fish abundance near Kodiak Island, Alaska

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Abstract—Humpback whales (*Megaptera novaeangliae*) are significant marine consumers. To examine the potential effect of predation by humpback whales, consumption (kg of prey daily) and prey removal (kg of prey annually) were modeled for a current and historic feeding aggregation of humpback whales off northeastern Kodiak Island, Alaska. A current prey biomass removal rate was modeled by using an estimate of the 2002 humpback whale abundance. A historic rate of removal was modeled from a prewhaling abundance estimate (population size prior to 1926). Two provisional humpback whale diets were simulated in order to model consumption rate. One diet was based on the stomach contents of whales that were commercially harvested from Port Hobron whaling station in Kodiak, Alaska, between 1926 and 1937, and the second diet, based on local prey availability as determined by fish surveys conducted within the study area, was used to model consumption rate by the historic population. The latter diet was also used to model consumption by the current population and to project a consumption rate if the current population were to grow to reach the historic population size. Models of these simulated diets showed that the current population likely removes nearly 8.83×10^6 kg of prey during a 5-month humpback whale feeding season, which could include around 3.26×10^6 kg of juvenile pollock (*Theragra chalcogramma*), 2.55×10^6 kg of capelin (*Mallotus villosus*), if these species are consumed in proportion to their availability. The historic humpback whale population may have removed over 1.76×10^7 kg of prey annually.

Manuscript submitted 22 April 2004 to the Scientific Editor's Office.
Manscript approved for publication 25 April 2005 by the Scientific Editor.
Fish. Bull. 104:10–20 (2006).

Numerous studies have revealed that an increased awareness of trophic-level interactions is essential in assessing the status of complex marine ecosystems (Overholtz et al., 1991; Hairston and Hairston, 1993; Pascual et al., 1993; Estes, 1994; Kenney et al., 1997; Trites et al., 1997). Such studies have shown that predator-prey relationships in marine systems can have direct and indirect effects on all ecosystem members, but predictions of their effects cannot be made without multispecies models.

Cetaceans are top predators in marine ecosystems and consume significant amounts of prey. Knowledge of the distribution, abundance, and foraging habits of cetaceans is, therefore, an essential element of any pelagic ecosystem study (van Franeker, 1992). Many species preyed upon by cetacean populations are targeted by other marine predators and commercial fisheries or are linked to fisheries through complex food webs. Previous studies have reported that prey removal due to cetacean consumption approaches or exceeds removals due to commercial fishing (Laws, 1977; Laevastu and Larkins, 1981; Bax, 1991, Markussen et al., 1992; Nordøy et al., 1995; Kenney et al., 1997). Such high levels of consumption can have significant effects on the distribution and abundance of prey species and the structure of marine communities (Perez and McAlister, 1993; Kenney et al., 1997; Croll et al., 1998). Therefore, examining consumption by cetaceans contributes information about complex ecosystem relationships and the long-term sustainability of marine resources (Perez and McAlister, 1993; Kenney et al., 1997; Tamura and Ohsumi[1]).

Humpback whales (*Megaptera novaeangliae*) feed in the waters off Kodiak Island and, because they are considered apex predators, may influence the structure of the Kodiak Island marine ecosystem (Fig. 1) (Trites et. al., 1997; Croll et. al., 1998). Modeling the amount of prey consumed (kg of prey annually) by feeding humpback whales is, therefore, a useful tool for evaluating their role as marine predators.

Cetaceans, in general, are described as opportunistic in their food selection, although species tend to select broad categories of prey such as cephalopods, fish, or zooplankton (Tomilin, 1954; Nemoto, 1959; Klumov, 1966; Sigurjónsson and Víkingsson, 1998). Humpback whales are classified as generalists and target a wide variety of prey species (Nemoto, 1970; Perry et al., 1999). They have been shown to be seasonal feeders on euphausiids (*Thysanoessa* spp.) and schooling fish species up to 30 cm in length, including capelin (*Mallotus villosus*), Pacific herring (*Clupea pal-*

[1] Tamura, T., and S. Ohsumi. 2000. Regional assessments of prey consumption by marine cetaceans in the world. International Whaling Commission document SC/52/E6, 45 p. Website: www.icrwhale.org/eng/SC52E6.pdf [Accessed on 30 November 2002].

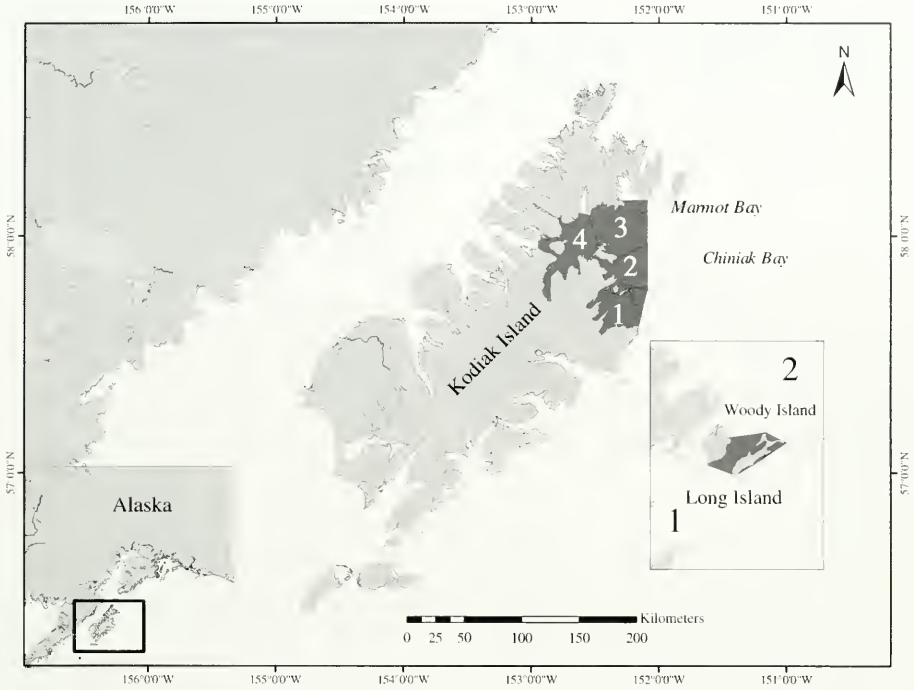

Figure 1

Map of Kodiak Island study area. Study area is shown as shaded area and subareas (1–4) are outlined and numbered. In detail is the nearshore subarea between Woody Island and Long Island.

lasi), walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius),* cod (*Gadus* spp.), sardines (*Sardinops* spp.), and sandlance (*Ammodytes* spp.) (Nemoto, 1957, 1959; Mitchell, 1973; Payne et al., 1990). The variety, as well as the amount, of prey removed from Kodiak waters may therefore be significant. Resource removal from Kodiak waters is of particular importance when considering the high value of Kodiak Island commercial fisheries, which totaled 63.3 million dollars in exvessel (wholesale) value in 2002 (NMFS[2]).

Modeling consumption by humpback whales as they recover from severe population declines could shed light on patterns of change seen in prey and sympatric consumer populations, such as marine birds and pinnipeds (Merrick, 1997; Anderson and Piatt, 1999). Commercial whaling in the 1900s significantly reduced the number of humpback whales, both within coastal Kodiak waters and throughout the North Pacific (Rice, 1978). Following the protection of humpback whales in 1965, however, their numbers in the central North Pacific increased, possibly by as much as 10%, between the early 1980s and early 1990s for some North Pacific stocks (Baker and Herman, 1987; Calambokidis et al.[3]). Removal and subsequent recovery of a marine predator of this magnitude may cause large variations in the biomass removal of prey in the ecosystem, as has been hypothesized in other studies (Laws, 1985; Springer et al., 2003). However, no empirical evidence exists to demonstrate such trophic interactions in the Gulf of Alaska. In this article,

[2] NMFS (National Marine Fisheries Service). 2002. Unpubl. data. Website: http://www.st.nmfs.gov/pls/webpls/MF_LPORT_YEARD.RESULTS [Accessed on 31 May 2003.]

[3] Calambokidis, J., G. H. Steiger, J. M. Straley, T. Quinn, L. M. Herman, S. Cerchio, D. R. Salden, M. Yamaguchi, F. Sato, J. R. Urbán, J. Jacobson, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dalheim, N. Higashi, S. Uchida, J. K. B. Ford, Y. Miyamura, P. Ladron de Guevara, S. A. Mizroch, L. Schlender, and K. Rasmussen. 1997. Abundance and population structure of humpback whales in the North Pacific basin. Cascadia Research Cooperative Final Contract Report 50ABNF500113 to Southwest Fisheries Science Center, La Jolla, CA 92038, 72 p. Website: http://www.cascadiaresearch.org/reports/rep-NPAC.pdf. [Accessed on 19 April 1999.]

we model the historic and current consumption rate by humpback whales within waters of northeastern Kodiak Island in order to assess the impact these whales have as predators on local prey populations.

Materials and methods

Study area

The study area encompassed waters of northeastern Kodiak Island, including Chiniak and Marmot Bays (Fig. 1). The study area was divided into four subareas of approximately equal size in order to equalize sampling effort and maximize coverage of the study area. Subareas were also used to separate sightings of humpback whales for the purpose of weighting diet composition in relation to prey availability. An additional subarea, including the waters near Woody and Long Islands, was not considered a survey subarea but was designated in the poststudy period for calculating diet composition ("nearshore," Fig. 1).

Sightings and abundance of humpback whales

Data on humpback whale sightings were collected during vessel surveys conducted between June and September in 2001 and 2002. Individual whales were identified from photographs of the black and white pigment patterns (and other natural markings) on the ventral surface of their tail flukes (Katona et al., 1979). A humpback whale sighting was defined as a sighting of an individual whale on a single day. Therefore, no whale was counted twice on one day, but may have been counted multiple times during the study period. Humpback whale sightings were summed by month and then by subarea for calculation of whale diet (see "Materials and methods" section: "Composition of simulated diets").

These sightings and fluke photographs were used in an associated study to estimate current humpback whale abundance within the study area (Witteveen, 2003). The estimate determined from this associated study was used in conjunction with historic catch data from the Port Hobron whaling station to estimate historic humpback whale abundance. The whaling grounds of Port Hobron encompassed most of eastern Kodiak waters—an area approximately four times that of the study area. To account for the size difference between whaling grounds and the study area, catch values were divided by four under the assumption of a random harvest throughout the grounds. The prewhaling and current estimates of humpback whale population size in the study area are 343 individuals (95% CI: 331, 376) and 157 individuals (95% CI: 114, 241), respectively (Witteveen, 2003).

Composition of simulated diets

Two diets were simulated: one that reflected the historic diet and the other that reflected the current diet for humpback whales. The diets were simulated because direct observation of humpback whale feeding behavior is rare and, even when observed, cannot produce a precise account of the prey species being eaten.

Diet A simulated historic target species and was based on the stomach contents of 39 humpback whales harvested at the Port Hobron whaling station from southeast Kodiak waters between 30 May and 9 August 1937 as analyzed by Thompson (1940).

Diet B simulated current target species and assumed no prey selectivity. It was based on the assumption that humpback whales will eat prey of a suitable size (<30 cm) in proportion to the relative occurrence of the prey in areas used by humpback whales. Euphausiid proportions in the diet were based on historic stomach contents and assumed to be constant over time (no current euphausiid abundance estimate is available).

Information on seasonal prey availability was collected from mid-water trawl surveys that were conducted within eastern Kodiak waters in July 2001 and from June through September 2002. Multiple passes with a commercial mid-water trawl net with a 22-mm mesh codend liner were made through acoustic scattering layers, ensuring an accurate representation of mid-water fish composition and occurrence. Species composition, species counts, and fish size were determined for each tow and grouped within the study subareas. Only data from tows conducted during the study period in 2001 and 2002 in areas utilized by humpback whales were included in our analysis. Therefore, prey surveys overlapped humpback whale sightings both temporally and spatially. A separate series of acoustic and purse-seine (center panel with a 3.2-mm mesh net) surveys was used to determine prey availability within the nearshore subarea from June through September 2002 (Foy[4]). Prey composition determined by these surveys was assumed to be homogeneous throughout the nearshore habitat within the study area.

To calculate diet B, the occurrence of fish smaller than 30 cm was determined from the mid-water trawl surveys within each subarea and month for both 2001 and 2002. Tow data were first separated by subarea and month. Percent composition of prey species in each tow was calculated by dividing the total number of fish of each species caught by the total number of all fish caught in each tow, excluding species larger than 30 cm (Nemoto, 1959) and species that were not previously documented as prey, such as flatfish and other nonschooling fishes (Nemoto, 1957, 1959; Klumov, 1963; Krieger and Wing, 1984, 1986; Perry et al., 1999).

To calculate diet B for the entire study area, prey proportions were weighted by the number of whales in each subarea. The weighted proportions were then summed across all months and subareas and multiplied by one minus the percentage of assumed euphausiid

[4] Foy, R. 2002. Unpubl. data. Fishery Industrial Technology Center, University of Alaska Fairbanks, Kodiak, AK 99615.

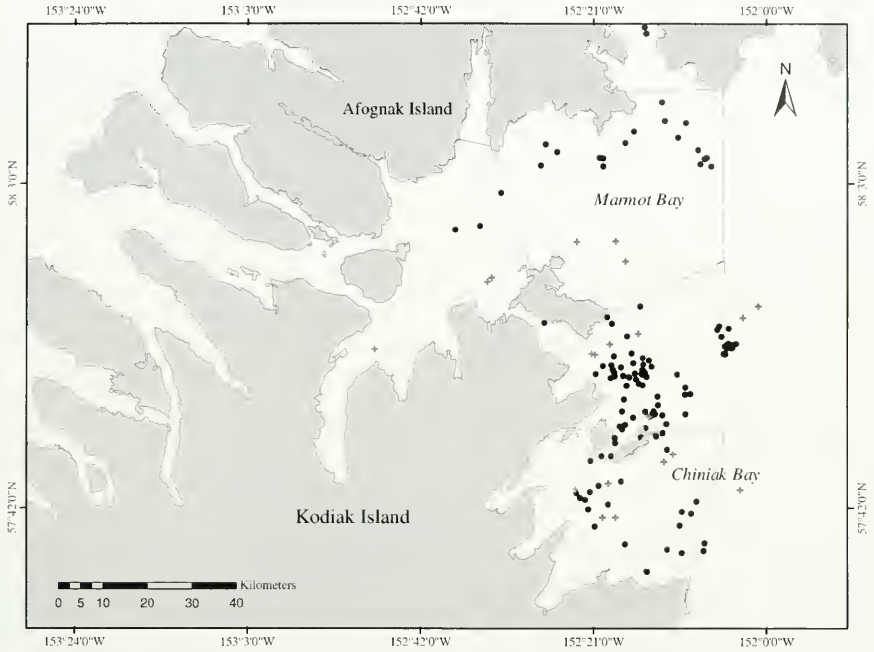

Figure 2

A close-up of the study area showing locations of humpback whale (*Megaptera novaeangliae*) sightings and prey tows (+) for 2001 and 2002. Only mid-water trawl locations are shown.

occurrence within the diet. Thus, diet B simulated a weighted availability of prey species based on temporal and spatial overlap between prey surveys and humpback whale sightings within the study period (Fig. 2).

Consumption rate

A seasonal consumption rate was estimated for both the current humpback whale population and the prewhaling humpback whale population. The prewhaling consumption rate was estimated by using diet A only. Diet B was used to estimate the consumption rate by the current humpback whale population and to project the consumption rate by a humpback whale population at the prewhaling abundance level.

The active metabolic rate (kcal/day) of feeding humpback whales was estimated in this study as $E=192M^{0.75}$, where Kleiber's (1961) model for basal metabolic rate (BMR; $E=70M^{0.75}$) was modified by using average oxygen consumption estimates for feeding baleen whales, where M is average body weight (kg) (Wahrenbrock et al., 1974: Sumich, 1983; Perez and McAlister, 1993).

Daily prey consumption was then estimated as

$$I = \frac{E}{K}\frac{1}{1{,}000},$$

where I = total prey consumption (kg/day);
E = estimated daily energy requirements (kcal/day); and
K = the estimated energy density (kcal/gram wet weight) of presumed prey.

The average body mass for humpback whales (M) was set equal to 30,408 kg (Trites and Pauly, 1998). The total energy density (K) of each diet was calculated by multiplying the average seasonal energy density of each prey species sampled in the study area by the percentage of that species within each diet and summing across all species. Values of K for individual prey species came from proximate compositions that were determined from prey collected during 2002 trawl surveys for all months within the study period (Foy[4]). For each month, energy density was calculated by multiplying percent lipid by 9.4 kcal/g and percent protein by 4.3 kcal/g, which are conversion factors based on heat produced during metabolism of food (Schmidt-Nielson, 1997). Carbohydrates were considered to be bound and not available for nutrition (Gaskin,

1982). The average seasonal energy density of each prey species was calculated by summing all values of energy density and dividing by the number of months in the study period. Previously published proximate composition values for surf smelt (*Hypomesus pretious*) and energy density data for euphausiids (*Thysanoessa* spp.) were used (Davis et al., 1997; Payne et al., 1999).

Seasonal prey consumption for the population was estimated by multiplying I by estimates of abundance (N) and the total number of days in the humpback whale feeding season. Consumption estimates were calculated for both the upper and lower 95% confidence limits on the abundance estimates to show a possible range of consumption. The length of the feeding season was presumed to be 152 days (Perez and McAllister, 1993).

Table 1

Number of sightings of humpback whales (*Megaptera novaeangliae*) for 2001 and 2002 by subarea and month in the Kodiak Island study area.

	2001 and 2002				
Area	June	July	August	September	Total
1	10	7	10	3	30
2	29	89	22	3	143
3	20	8	0	12	40
4	0	3	0	7	10
Nearshore	5	14	0	0	19
Total	64	121	32	25	242

Results

Analysis of sightings showed that humpback whales were not uniformly distributed within the study area (Table 1). Occurrence of humpback whales within subareas was variable, indicating within-season shifts of habitat use. Peak humpback whale sightings occurred in subarea 2 in July of both years. No humpback whales were sighted in the nearshore area after the month of July in either year.

Only two prey items were identified in the 27 stomachs that contained appreciable quantities of prey of 39 stomachs analyzed by Thompson (1940). Surf smelt were found in 21 of 27 (78%) stomachs and euphausiids were found in 6 of 27 (22%) stomachs (Table 2). These percentages represent diet A. Energy densities of these two species combined to give a total energy density of 1.31 kcal/gram (Table 3).

The fish species in areas used by humpback whales in 2001 and 2002, as shown by mid-water trawl surveys, were pollock (36.96%), capelin (28.89%), eulachon (7.60%), Pacific sandlance (4.44%), Pacific sandfish (0.08%), and Pacific herring (0.03%) (Table 2). These percentages represent diet B. Calculated energy densities of prey species ranged from a high (eulachon) of 2.52 kcal/gram to a low of 1.12 kcal/gram (juvenile pollock). The total energy density for diet B was 1.19 kcal/gram (Table 3).

Based on energetic content of the above diets, the model indicated that each humpback whale in the study area would consume 338 kg/day on diet A and 370 kg/day on diet B. Using a prewhaling estimate of 343 (95% CI=331–376) animals in the study area, we determined that humpback whales feeding on diet A prior to 1927 would have removed an estimated 1.76×10^7 kg of prey annually (95% CI= 1.70×10^7 to 1.93×10^7), including nearly 3.87×10^6 (3.74×10^6 to 4.24×10^6) kg of euphausiids and approximately 1.37×10^7 (1.32×10^7 to 1.50×10^7) kg of surf smelt (Table 4). If diet B accurately reflects prey selection by the estimated 157 (95% CI=114–241)

Table 2

Composition and relative occurrence of prey species represented in simulated humpback whale (*Megaptera novaeangliae*) diet A (historic) and diet B (current).

Diet	Prey species	Common name	Percent of total diet
A	*Hypomesus pretious*	surf smelt	78.00%
	Thysanoessa spp.	euphausiid spp.	22.00%
		Total	100%
B	*Theragra chalcogramma*	walleye pollock	36.96%
	Mallotus villosus	capelin	28.88%
	Thysanoessa spp.	euphausiid spp.	22.00%
	Thaleichthys pacificus	eulachon	7.60%
	Ammodytes hexapterus	Pacific sandlance	4.44%
	Trichodon trichodon	Pacific sandfish	0.08%
	Clupea harengus pallasi	Pacific herring	0.03%
		Total	100%

Table 3

Monthly and average energy densities (kcal/gram) of prey species represented in simulated humpback whale (*Megaptera novaeangliae*) diets A and B based on lipid and protein composition. Energy densities were used to estimate consumption by humpback whales. Average values in parentheses have been adjusted to reflect standard deviations of lipid and protein composition. N/A = not available.

	Energy densities (kcal/gram)				
Species	June	July	August	September	Average
Capelin	1.1285	1.2632	1.1956	1.4298	1.2542 (1.1665, 1.3755)
Pacific sandlance	1.4179	1.4179	1.4179	1.4179	1.4179 (1.3211, 1.5590)
Pacific sandfish	0.8661	1.2126	1.1165	1.1165	1.0779 (1.0449, 1.1300)
Eulachon	2.1582	2.5218	2.6758	2.7424	2.5245 (2.3761, 2.6860)
Herring	2.0999	2.0999	1.9454	2.1205	2.0664 (1.9432, 2.2942)
Juvenile pollock	1.0144	1.0657	1.1380	1.2461	1.1160 (0.9730, 1.2994)
Euphausiids	N/A	N/A	N/A	N/A	0.7430
Surf smelt	N/A	N/A	N/A	N/A	1.4698

Table 4

Daily and annual (over a 152-day feeding season) consumption of prey from two different diets off northeastern Kodiak Island by humpback whales (*Megaptera novaeangliae*) at two levels of population abundance: the current population of 157 and the historic population of 343 (also presumed to be the carrying capacity to which the current population will recover). Diet A is the simulated diet of the historic population through analysis of stomach contents of 39 whales in 1937; Diet B is the simulated diet of the historic and current population based on currently available prey of suitable size for consumption.

		Annual prey removal (kg)		
Prey species	Daily prey removal (kg)	Mean	Lower limit	Upper limit
Historic population				
Diet A				
Surf smelt	90,301	13,725,715	13,245,515	15,046,264
Euphausiids	25,469	3,871,355	3,735,914	4,243,818
Total	115,770	17,597,070	16,981,429	19,290,083
Diet B				
Euphausiids	27,934	4,246,006	4,097,458	4,654,514
Walleye pollock	46,924	7,132,406	6,882,876	7,818,614
Capelin	36,671	5,573,943	5,378,936	6,110,211
Eulachon	9,652	1,467,057	1,415,731	1,608,202
Pacific sandlance	5,635	856,475	826,511	938,876
Pacific sandfish	98	14,907	14,386	16,342
Pacific herring	33	5,038	4,862	5,523
Total	126,974	19,300,028	18,624,808	21,156,882
Current population				
Diet B				
Euphausiids	12,786	1,943,507	1,411,209	2,983,345
Walleye pollock	21,478	3,264,687	2,370,537	5,011,399
Capelin	16,785	2,551,338	1,852,564	3,916,385
Eulachon	4,418	671,510	487,593	1,030,789
Pacific sandlance	2,579	392,031	284,659	601,780
Pacific sandfish	45	6,824	4,955	10,474
Pacific herring	15	2,306	1,675	3,540
Total	58,119	8,834,124	6,414,587	13,560,661

humpback whales currently feeding in the study area, these whales would be removing nearly 8.83×10^6 (6.41×10^6 to 1.36×10^7) kg annually, including 3.26×10^6 (2.37×10^6 to 5.01×10^6) kg of pollock, nearly 2.55×10^6 (1.85×10^6 to 3.92×10^6) kg of capelin, and 6.71×10^5 (4.88×10^5 to 1.03×10^6) kg of eulachon. If the same diet were consumed by a population of humpback whales allowed to return to prewhaling abundance, the projected population would remove 1.9×10^7 (1.86×10^7 to 2.12×10^7) kg of prey annually, including approximately 7.13×10^6 (6.88×10^6 to 7.82×10^6) kg of pollock, 5.57×10^6 (5.38×10^6 to 6.11×10^6) kg of capelin, and 4.25×10^6 (4.10×10^6 to 4.65×10^6) kg of euphausiids (Table 4).

Discussion

Consumption rate

Estimating the energy requirements of large cetaceans is inherently difficult and values presented in the present study may be subject to substantial uncertainty. Previous studies in which consumption rates for cetaceans were estimated have used a range of values to adjust BMR ($E=70M^{0.75}$) for active metabolism. These values generally range from approximately 1.5 to 3 times BMR (Hinga, 1979; Lockyer, 1981; Sigurjónsson and Víkingsson, 1998). Our value of 192 is 2.7 times larger than 70 and is, therefore, a reasonable estimate because it fits within this range and is based on the observed oxygen consumption rates of baleen whales. However, the consumption estimates are highly sensitive to perturbations of model input; a 5% error in this value would cause deviation of the same percentage (5%) in final consumption values. Further, all values in our consumption model are assumed to be constant when body mass, physiological status, and assimilation efficiency are likely subject to large seasonal fluctuations (Innes et al., 1987; Perez and McAlister, 1993, Kenney et al., 1997; Trites et al., 1997; Sigurjónsson and Víkingsson, 1998). Our model, however, did account for seasonal changes in the energy density of local prey sources; previous models, on the other hand, did not account for these changes (Perez and McAlister, 1993). Further research is necessary to obtain reliable field estimates of metabolic rates if model uncertainty is to be reduced.

The historic prevalence of surf smelt in diet A could imply a dramatic change in surf smelt availability, misidentification, or an overestimation of smelt found in stomachs. Thompson's (1940) analysis resulted from "samples of stomach contents" obtained from catcher vessels; therefore, these samples may have completely missed less prevalent species. Further, stomach samples may have only reflected the most recent meal of the whale and therefore be biased toward a single species. This potential bias, however, could have been minimized by sampling stomachs throughout the season (May 30–August 09) (Thompson, 1940). Diet B was dominated by walleye pollock, a species not present in historic diet A. The increased importance of juvenile pollock in contemporary humpback whale diet B could reflect changes in prey species availability and use, foraging selectivity, or reflect our diet reconstruction method.

Diet B is considered provisional for two reasons. First, it is assumed that humpback whales eat prey species in proportion to their availability within foraging areas. Humpback whales select preferred prey species and consumption, therefore, may be disproportional to availability. That is, they may be selectively foraging from all available prey sources. Previous foraging studies have described humpback whale distribution as being correlated with areas of capelin (Whitehead and Carscadden 1985; Piatt et al. 1989) and sandlance abundance (Payne et al. 1986; Kenney et al. 1996) and this correlation may indicate a possible preference for small forage fish species. Given that in the decades since whaling, the Gulf of Alaska has shifted from a system dominated by forage fish to one dominated by pollock and other groundfish (Merrick 1997; Anderson and Piatt 1999; Benson and Trites 2002), a shift in prevalence from surf smelt in the historic diet to pollock in the current diet is not unexpected. Pollock have been shown to be a dominant prey source of humpback whales harvested in Russia (Klumov, 1963). Additionally, humpback whales in southeastern Alaska have been observed near schools of juvenile pollock and are believed to eat pollock to an unknown, but potentially large, extent in some years (Gabriele[5]).

The second source of uncertainty in diet B stems from the assumption that our mid-water trawl surveys provide unbiased samples of all available prey. Because these surveys were not designed to sample zooplankton, they may have produced a biased estimate of euphausiid availability. This bias may not be significant, however, because the 22% value we used in diet B was based on historic usage and falls within the range of euphausiid consumption (5–30% of the total diet) estimated in other humpback whale studies (Perez and McAlister, 1993; Kenney et al., 1997).

Further, diet B was constructed from the results of mid-water trawl surveys that may underestimate the availability of some forage fishes, particularly Pacific sandlance. Pacific sandlance are often small enough to swim through the meshes in the net or are found in benthic habitats and cannot be captured by mid-water trawl methods. To minimize this potential sampling bias, we supplemented our trawl surveys with purse seine sampling in the nearshore subarea. Despite this effort we may have underestimated the prevalence of Pacific sandlance in the area because it was found to dominate the diets of other coastal piscivores; stomach contents of 34 coho salmon (*Oncorhynchus kisutch*) and Pacific halibut (*Hippoglossus stenolepis*) in 2002 (Witteveen[6]) and regurgitants from blacklegged kittiwakes

[5] Gabriele, C. 2001–2002. Personal commun. Glacier Bay National Park, P.O. Box 140, Gustavus, AK 99826-0140.

[6] Witteveen, B. H. 2002. Unpubl. data. Fishery Industrial Technology Center, University of Alaska Fairbanks, Kodiak, AK 99615.

in 2001 (n=96) and 2002 (n=147) were dominated by Pacific sandlance (Murra et al., 2003).

Ecological effects from humpback whale prey consumption

Although estimates of consumption are highly dependent on estimates of population abundance and metabolic rates, these values indicate that humpback whales were, and still are, significant predators within the Kodiak Island ecosystem.

Historic commercial whaling reduced the population in our study area to an estimated low of 27 animals by 1938 (Witteveen, 2003). The removal of so many large consumers likely had significant impacts on the surrounding ecosystem. As modeled, reducing historic consumption to that of current levels would release nearly 10,000 tons of prey within the study area in a single feeding season. Such a release could have caused a trophic cascade effect.

Cetacean removals in the Southern Ocean have demonstrated how trophic cascades can affect marine ecosystems through removal of large marine predators, including whales (Laws, 1985). It has been hypothesized that a similar reorganization of the marine community may have occurred in the Bering Sea and Gulf of Alaska, although the mechanisms of such a cascade are not well understood (Merrick, 1997; Trites, 1997; Springer et al. 2003). Removal of whales during commercial harvest reduced predation on certain fish, cephalopod, and zooplankton species, which were then available to other consumers. This large number of unconsumed prey, when combined with environmental factors such as the 1977 regime shift, may have contributed to the growth of sympatric marine predator populations from the late 1940s to late 1970s. It is hypothesized that whale stock resurgence, coupled with the 1977 regime shift that favored the proliferation of groundfish species, may have reduced prey availability to other piscivores in the system and may have led to declines seen in harbor seal (*Phoca vitulina*), Steller sea lion, northern fur seal (*Callorhinus ursinus*), common murre (*Uria aalge*), thick-billed murre (*U. lomvia*), and red-legged kittiwake (*Rissa brevirostris*) populations (Merrick, 1995, 1997; NRC, 1996; Trites, 1997). The Gulf of Alaska and Bering Sea ecosystems may still be affected by changes caused by baleen whale removals and their recovery (NRC, 1996).

Assuming that the Kodiak Island study area was similarly affected by this trophic reorganization, an estimate of the current consumption by humpback whales would help elucidate the role that a humpback whale recovery is playing in ecosystem dynamics. If our diet composition and subsequent consumption estimates are accurate, our results indicate that the diet of humpback whales in Kodiak waters directly overlaps those of sympatric piscivores and the biomass that is removed may be substantial. The top species modeled in the humpback whale diet represent important sources of energy for multiple higher-trophic-level species and are known to be significant dietary species for Steller sea lions (Wynne[7]), harbor seals (Jemison[8]), tufted puffins (*Fratercula cirrhata*) (Piatt et al., 1997), blacklegged kittiwakes (Murra et al., 2003), adult pollock, Pacific halibut, and arrowtooth flounder (Livingston, 1993; Yang, 1995; Merrick, 1997; Best and St. Pierre[9]).

Our model indicates that humpback whales within the study area may currently be consuming a significant amount of fish, including over 3.26×10^6 kg of juvenile pollock and nearly 3.62×10^6 kg of small forage fish, such as capelin, eulachon and Pacific sandlance, during a 152-day feeding season. In comparison, tufted puffins consume less juvenile pollock (6.40×10^4 kg) between mid-July and mid-September, but this amount still accounts for one-tenth of the age-0 pollock stock in the Gulf of Alaska during early July (Hatch and Sanger, 1992). In addition, gadid removal by Steller sea lions in 1998 was estimated to be 1.79×10^8 kg, or 12% of the total gadid biomass that is removed by commercial fisheries for that year (Winship and Trites, 2003). This amount, although nearly 55 times the amount of pollock removal due to consumption by humpback whales, includes all gadid (not only pollock) species removals in all Alaskan waters. More importantly, these fish are likely larger (≥60 cm vs. ≤30 cm) than fish targeted by humpback whales.

Although humpback whales generally feed on smaller age classes than are targeted by commercial fisheries or Steller sea lions (Perez and McAlister[1]; Kenney et al., 1997), consumption of younger age classes may affect future recruitment into the fishery. Barrett et al. (1990) stated that consumption of young cod (*Gadus morhua*) and saithe (*Pollachius virens*) by shags (*Phalacrocorax aristotelis*) and cormorants (*P. carbo*) in the Northeast Atlantic could be a limiting factor in recruitment in years of low stock size, even if consumption of these species was overestimated by an order of magnitude. Thus, it is noteworthy that the removal by humpback whales of an estimated 3.26×10^6 kg of pollock (age 0–2) equals 30% of the 2002 commercial pollock harvest of 1.09×10^7 kg (ages 3 to 8) for the entire Kodiak Island management area and 2.1% of the 2002 spawning biomass of pollock for the entire Gulf of Alaska, which was estimated at 1.58×10^8 kg (NMFS[10]; NPFMC[11,12]).

These comparisons are based on mean estimates of prey removal and do not take into account model uncer-

[7] Wynne, K. M. 2002. Unpubl. data. Fishery Industrial Technology Center, Univ. Alaska Fairbanks, Kodiak, AK 99615.

[8] Jemison, L. A. 2001. Summary of harbor seal diet data collected in Alaska from 1990–1999. *In* Harbor seal investigations in Alaska (R. J. Small, ed.), p. 314–22. Ann. Rep. NOAA Grant NA 87Fx0300. Alaska Departmart of Fish and Game, P.O. Box 240020, Douglas, AK 99824.

[9] Best, E. A., and G. St. Pierre. 1986. Pacific halibut as predator and prey. International Pacific Halibut Commission Technical Report 21, 27 p. Website: http://www.iphc.washington.edu/halcom/pubs/techrep/tech0021.pdf. [Accessed on 31 May 2003.]

[10, 11, 12] *See next page for footnote text.*

tainty. When uncertainty is considered, comparison to even the lower end of estimates of prey removal are still of note. For example, assuming that removal of juvenile pollock is equal to the lower estimate, or 2.37×10^6 kg, the removal of pollock by humpback whales could still equal 21.7% of the 2002 commercial pollock catch and 1.5% of 2002 spawning biomass. Thus, it follows that if true consumption is actually closer to the upper estimates, the impact of prey removal by humpback whales would likely increase.

The humpback whale represents only one of a myriad of marine consumers within the Kodiak Island ecosystem whose ecological role cannot be determined without sophisticated multispecies models and an analysis of ecosystem interactions. This study was designed to provide essential baseline data and a model for estimating prey removal by foraging humpback whales. Our results show that the potential for biomass removal due to consumption by humpback whales is significant and that the foraging strategies of these whales warrant further investigation. Continued research efforts can improve estimates of biomass removal by identifying target prey, determining the degree of prey selectivity, and assessing variable foraging efficiency.

Acknowledgments

The authors are grateful for the insight and guidance provided by Janice M. Straley, Terry J. Quinn II, Brendan P. Kelly, and Chris Gabriele. Field and laboratory assistance was provided by Lisa Baraff and Katie Brenner. Financial support for this project was provided by the Rasmuson Fisheries Research Center and NOAA Grant no. NA16FX1270 to the University of Alaska Gulf Apex Predator-Prey Project. All research was conducted until provisions of NMFS Scientific Research Permit 473-1433.

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Variation in trawl geometry due to unequal warp length

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Abstract—Survey standardization procedures can reduce the variability in trawl catch efficiency thus producing more precise estimates of biomass. One such procedure, towing with equal amounts of trawl warp on both sides of the net, was experimentally investigated for its importance in determining optimal trawl geometry and for evaluating the effectiveness of the recent National Oceanic and Atmospheric Administration (NOAA) national protocol on accurate measurement of trawl warps. This recent standard for measuring warp length requires that the difference between warp lengths can be no more than 4% of the distance between the otter doors measured along the bridles and footrope. Trawl performance data from repetitive towing with warp differentials of 0, 3, 5, 7, 9, 11, and 20 m were analyzed for their effect on three determinants of flatfish catch efficiency: footrope distance off-bottom, bridle length in contact with the bottom, and area swept by the net. Our results indicated that the distortion of the trawl caused by asymmetry in trawl warp length could have a negative influence on flatfish catch efficiency. At a difference of 7 m in warp length, the NOAA 4% threshold value for the 83-112 Eastern survey trawl used in our study, we found no effect on the acoustic-based measures of door spread, wing spread, and headrope height off-bottom. However, the sensitivity of the trawl to 7 m of warp offset could be seen as footrope distances off-bottom increased slightly (particularly in the center region of the net where flatfish escapement is highest), and as the width of the bridle path responsible for flatfish herding, together with the effective net width, was reduced. For this survey trawl, a NOAA threshold value of 4% should be considered a maximum. A more conservative value (less than 4%) would likely reduce potential bias in estimates of relative abundance caused by large differences in warp length approaching 7 m.

Manuscript submitted 20 October 2004 to the Scientific Editor's Office.
Manuscript approved for publication 6 June 2005 by the Scientific Editor.
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Standardization of trawl survey procedures can reduce the variability in abundance indices between samples, survey vessels, and over time by reducing the variability in trawl catch efficiency. Such standardization was the focus of the recently developed U.S. National Oceanic and Atmospheric Administration (NOAA) protocols for the operation of its groundfish bottom trawl surveys (Stauffer, 2004). The first of these protocols concerns the measurement of towing cables or warps. For vessels towing with two warps, the NOAA protocols specify that the difference in length between port and starboard warps may not exceed 4% of the wire length between otter doors measured along the bridles and footrope. The need for adopting such a critical value was considered essential because of the belief that unequal warp lengths—from inaccurate measurement or subsequent stretching—would lead to distortion of trawl geometry and a change in catch efficiency, particularly for operations that use trawl winches with the brakes set or locked. The adopted value, however, was chosen somewhat arbitrarily because experimental data showing the dependency of trawl geometry or fishing performance on warp symmetry was lacking for any of the bottom trawl surveys subject to the protocols.

In this study, we examine the effect of unequal warp lengths on the geometry of the 83-112 Eastern trawl which is used by the Alaska Fisheries Science Center (AFSC) to conduct the annual eastern Bering Sea shelf survey. Although we monitor a full suite of trawl dimensions, such as door spread, wing spread, and headrope height that are typically measured on trawl surveys, our attention was primarily focused on the distance between the footrope and lower bridles with the sea floor. Prior studies with this trawl have demonstrated that escapement under the footrope (Somerton and Otto, 1999; Munro and Somerton, 2002; Weinberg et al., 2004) and herding by the bridles (Somerton and Munro, 2001) are the most important determinants of catch efficiency for flatfishes and other benthic species. Although we understand that catch efficiency depends on animal behavior as well as trawl geometry, a goal of our study was to assess whether the 4% critical value is appropriate to prevent an appreciable degradation of catch efficiency due to warp asymmetry, the result of unequal trawl warp lengths.

Materials and methods

Experimental design

The experiment was conducted during 14–17 September 2003 along the Alaska Peninsula in Bristol Bay approximately 85 km NE of Amak Island (55°58′N, 162°55′W) on smooth, relatively level bottom at a depth of 82 m. Trawling was performed with the chartered 38-m stern trawler FV *Vesteraalen*. The *Vesteraalen* is powered by a single 1725-hp engine and is equipped with split Rapp Hydema (Rapp Hydema AS, Bodø, Norway) trawl winches carrying 2.5 cm (1″) diameter, compacted, solid-core trawl warp.

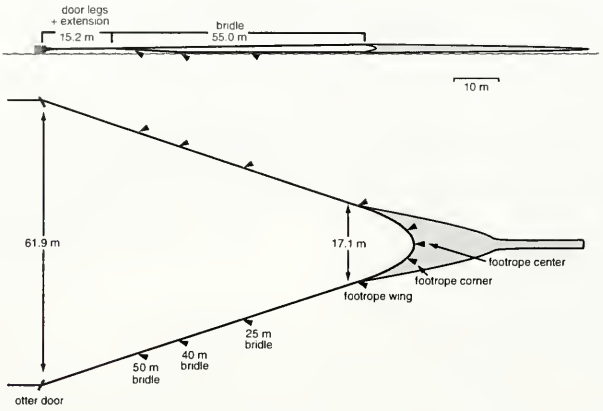

Figure 1

Schematic diagram of the 83-112 Eastern survey trawl and rigging shown from the side (upper panel) and from above (lower panel). The experimentally determined mean door spread and wing spread dimensions shown apply when towing at a depth of 82 m with 274 m of trawl warp on each side. Bottom contact sensor units, shown as oversized triangles along the bridles and footrope, are labeled by position as discussed in the text.

The 83-112 Eastern is a low-rise, 2-seam, flatfish trawl designed for use on smooth, soft bottom. The nylon net is constructed of 10.1-cm stretch mesh in the wing and body, 8.9 cm in the intermediate, and double 8.9-cm mesh lined with a 3.1-cm mesh in the codend. It is towed behind a pair of 1.8×2.7 m steel "V" doors, weighing approximately 816 kg apiece, which are attached to the net by two 3-m-long door legs (consisting of 1.6-cm long-link chain); a 12.2-m-long door leg extension (consisting of 1.9-cm diameter stranded wire); and a pair of 55-m-long, bridles (consisting of 1.6-cm diameter bare stranded wire) on each side of the net (Fig. 1). The 25.5-m-long (83 ft) headrope has 41 evenly spaced, 20.3-cm diameter floats that provide 116.4 kg of total lift. The 34.1-m-long (112 ft), 5.2-cm diameter footrope is constructed of 1.6-cm diameter stranded-wire rope protected by a single wrap of both 1.3-cm diameter polypropylene line and split rubber hose. The footrope is weighted with 51.8 m of chain (0.8-cm proof-coil) attached at every tenth link, forming 168 loops to which the netting is hung. An additional 0.6-m-long, 1.3-cm long-link chain extension connects each lower bridle to the trawl wing tips to help keep the footrope close to the bottom. Because the wire length between otter doors measured along the bridles and footrope is 175.6 m, the critical value for differential warp length for this trawl established by the NOAA 4% rule is 7 m.

Prior to the experiment, the warp length to be used was measured to the nearest 0.1 m with a calibrated, in-line wire counter (Olympic 750-N, Vashon, WA). A zero reference point was painted on each trawl warp, as determined by first setting the wire counter to zero with the trawl door just beneath the water surface and then measuring out 274 m (150 fm), the survey standard warp length for a fishing depth of 82 m. To verify this benchmark measurement, the process was repeated and all replicate measurements were found to be within 0.3 m, which is less than the 1 m specified by the NOAA trawl survey protocols for replicate measurements. Subsequent reference marks, measured by tape, were then placed along each warp at 3, 5, 7, 9, 11, and 20 m from the zero mark.

The experiment consisted of examining the effect of seven differences in warp length, henceforth referred to as "offsets," where one warp was positioned at values of 0, 3, 5, 7, 9, 11, or 20 m longer. An experimental set consisted of all seven offsets, chosen in random order. A treatment consisted of towing the trawl, with the winch brakes locked, at the specified offset for 5 minutes at 3 knots while maintaining a constant vessel heading. Treatments were preceded by a 2-min equalization period at the specified offset. A haul consisted of two treatment sets: one with a port offset and the other with a starboard offset—the order having been chosen randomly for each haul. To minimize the effect of bottom currents on trawl symmetry, hauls were made in pairs along the axis of the dominant current direction, either with or against the current—again, the order having been chosen randomly. This direction was determined by deploying a current meter (Nobska MAVS-3, Woods Hole, MA) 3 m above the bottom for one day

prior to the start of the experiment. Hauls were made with the trawl codend open to eliminate any catch effects on trawl geometry.

Several measures of trawl geometry and performance were taken during each treatment. The distance between the doors (door spread), the wing tips (wing spread), and the center of the headrope to the sea floor were measured acoustically with Scanmar sensors (Scanmar, Asgardstrand, Norway) to 0.1 m at 4-s intervals. Water flow, both perpendicular and tangential to the headrope, was measured to 0.1 knot at 24-s intervals with a Scanmar trawl speed sensor placed at the center of the headrope. Vessel position was measured with satellite navigation at 2-s intervals. Bridle tension was measured in kilograms at 2-s intervals using in-line tension recorders (Billings Ind. TR-999, N. Falmouth, MA) attached behind the door legs. Bottom current velocity in cm/s and direction data were recorded at 10-s intervals.

Footrope off-bottom distance was measured at five positions simultaneously by placing bottom contact sensors (BCS) at the center of the footrope, at the corners located 3 m to either side of the center, and on each wing 1 m behind the wing tip (Fig. 1). These sensors are self-contained units consisting of a tilt meter, which measured angle to the nearest half degree at 0.5 s elapsed time intervals, and a data logger housed in a watertight stainless steel container that fits inside a steel sled (Somerton and Weinberg, 2001). One side of this sled clips into a clamp on the footrope, which allows that end of the sled to pivot freely about the footrope while the other end drags along the bottom (Fig. 2). In this way, changes in the distance of the footrope from the bottom produced changes in the recorded tilt angle. Conversion from tilt angle to distance off-bottom was accomplished by applying a calibration function derived for each BCS unit by fitting a quadratic function to data from an experiment in which angles associated with known distances from a hard surface were measured. The BCS unit extended 44 cm behind the footrope and weighed (BCS, sled, and footrope clamp) 8.9 kg in seawater. The clamp extended beneath the footrope by 2 cm and, depending on the extent of penetration into the sediment, could raise the footrope off the bottom (Fig. 2). Because the degree of penetration is unknown, no adjustments to our calibration functions were made.

Figure 2

Bottom contact sensors shown mounted to the footrope (upper) and bridle (middle). The footrope shown in the "on-bottom" position without lateral tension and on a hard surface is elevated 2 cm by the footrope clamp (lower).

Bridle off-bottom distance was measured at six positions simultaneously by placing BCS units on the lower bridle at distances of 25, 40, and 50 m forward of the wing tip on both sides of the trawl (Fig. 1). However, the BCS units used on the bridles differed from those used on the footrope. These units were mounted on a triangular frame designed to hold the BCS perpendicular to the bridle (Fig. 2; Somerton, 2003). The triangular frame measured 49 cm in its longest dimension and was held in place by a cable stop that also extended beneath the bridle by about 2 cm. The weight of a bridle BCS unit and frame was 8.7 kg in seawater.

Data analyses

Three tilt angle measurements from each BCS unit were averaged for each 1.5-s interval, converted to distance off-bottom by applying the calibration function determined for that unit, and then the off-bottom distances

were averaged for each experimental treatment on each haul. Mean off-bottom distances for each bridle and footrope position, except the footrope center, were grouped by offset distance (i.e., long side vs. short side of an experimental treatment) where, for example, the distance measurements from the 25-m position on the starboard bridle collected on a starboard treatment (long side) was grouped with the measurements from the 25-m position on the port bridle during a port treatment. Under these groupings, we assumed equality and subsequently refer to the offsets by whether they were on the long or short side (e.g., long 5 m) rather than whether they were on the port or starboard side (e.g., port 5 m).

To allow interpolation between the experimental offsets, cubic spline models (Venables and Ripley, 1994) were fitted to door spread, wing spread, headrope height, and the off-bottom distances for each bridle and footrope position as a function of offset. Bootstrapped empirical 95% confidence intervals (CI; Efron and Tibshirani, 1993) were estimated for all measured categories as described in the following example for off-bottom distance as follows: 1) assuming that mean off-bottom distances within a set were correlated because of local environmental conditions, we chose 1000 bootstrap replicates by sampling entire sets of measurements with replacement; 2) we fitted a cubic spline, weighted by the inverse of the variance, to each bootstrap sample, and then predicted the mean off-bottom distance for each 1 m of offset; and 3) we ranked the predicted values, then chose the 25th highest and lowest values as the CI bounds. Similarly, we estimated the empirical 95% CIs about the mean off-bottom distance at zero offset in the same manner except that only zero offset treatments were considered.

Modeling trawl shape

To help visualize the distortion of the trawl that occurs in response to offset, we created three views of the trawl: 1) the shape of the lower bridle when viewed laterally, 2) the shape of the headrope when viewed from above, and 3) the shape of the footrope when viewed from in front of the trawl. In addition, we calculated the area swept by the bridles (herding area) and the effective net width (i.e., the greatest lateral dimension of the net).

Bridle shape and herding area

The shape of the lower bridle, when viewed laterally (i.e., off-bottom distance as a function of position along the bridles), was approximated by linear interpolation between the mean off-bottom distances measured at the wing, and the 25-, 40-, and 50-m bridle positions. Such shape functions were calculated for both the long side and the short side of the trawl at each offset increment.

The herding area can be considered as a function of the bridle contact length, that is, the length of the bridle that is sufficiently close to the bottom to elicit a herding response (Somerton and Munro, 2001) and the angle-of-attack between the bridle and the direction of travel (α). For flatfish, the vertical distance of the bridle from the sea floor at which a herding response is initiated (reaction height) will vary with species, size, viewing conditions, arousal state, and other variables, but for illustrative purposes, we considered a reaction height of 1 cm where video observations indicated that this value is appropriate for a small flatfish, initially at rest and unaware of the approaching bridle (Somerton, unpubl. data). Thus the value of the bridle contact length was determined as the distance between the wing tip and the point along the bridle at which the interpolated value of off-bottom distance reached the reaction height. The angle-of-attack, α, was not measured during the experiment; however, when the trawl is symmetric, α can be modeled as

$$\alpha = \mathrm{Sin}^{-1}\left(0.5(D-W)/B\right),$$

where D = the distance between doors;
W = the distance between wing tips; and
B = the distance between the wing tip and the door.

It is not clear, however, how α will differ between the long and short side of the trawl when warp offsets occur. For illustrative purposes, we assumed that α is symmetrical and remains constant during all experimental values of warp offset. Thus, for each side of the trawl and for each offset, a value of bridle contact length and α were first calculated as above, then the width of the herding area on each side of the trawl was computed as the bridle contact length times sin (α) and the two areas were summed together.

Headrope shape and effective net width

The curved shape of the headrope when viewed from above can be approximated as a quadratic (parabolic) function when the warps are equal in length and there are no external forces to distort the symmetry of the net (Fridman, 1969). If the shape remains parabolic as the warp offset is increased, then the headrope shape can be uniquely determined with three geometric measurements: 1) the length of the headrope; 2) the distance between wing tips; and 3) the tangent to the headrope at its center. The first quantity was measured at the start of the experiment. The second quantity was measured acoustically on all hauls, and then averaged by treatment. The third quantity was calculated as the quotient of the tangential water velocity (U) divided by the perpendicular velocity (V) measured by the headrope speed sensor (i.e., U/V). With these quantities, the headrope shape was determined as described in Appendix A.

Although the shape of the headrope determined by this method is assumed to be parabolic, the headrope becomes increasingly asymmetric about the direction of travel as the degree of warp offset increases because the wing tip on the short side of the net precedes that on the long side. When this distortion occurs, the mea-

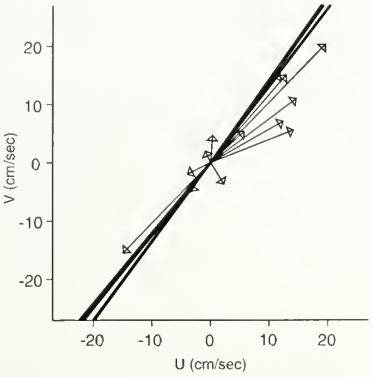

Figure 3

Current velocity vectors during each of the 13 experimental tows are shown with arrows. Vessel direction during these tows is shown with the dark lines. The axes, labeled U and V, indicate the latitudinal and meriodonial components of the velocity vectors in cm/s.

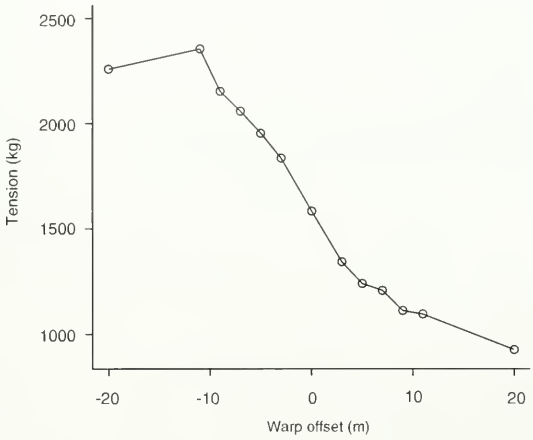

Figure 4

Mean tension (in kilograms) measured on both port and starboard door legs is shown plotted as a function of warp offset in meters. Note that on the side with the shorter warp (negative offset), tension is higher than when the warps are equal and that on the side with the longer warp, the tension is lower.

sured distance between wing tips becomes increasingly greater than the effective net width (i.e., the distance from wing tip to wing tip projected on a plane perpendicular to the direction of travel). The method used to estimate effective net width was based on headrope geometry and is described in Appendix A.

Footrope shape viewed from the net mouth

Because of footrope geometry, the importance of footrope bottom contact to overall net efficiency varies along the length of the footrope. This feature is true not only because escapement probability likely changes with the angle of the footrope in relation to the direction of travel but also because the proportion of the net width spanned by a unit length of footrope varies. To help visualize the latter effect better, we projected the off-bottom distances from their positions along the footrope onto a plane that was perpendicular to the direction of travel and spanned by the effective net width, using the footrope shape model determined for each offset increment described in Appendix A.

Results

Twelve successful tows consisting of 24 sets of treatments were completed during the experiment. Bottom current velocities ranged from about 5 cm/s to about 30 cm/s and current direction was approximately parallel to the trawl towing direction (Fig. 3); consequently the mean current velocity perpendicular to the towing direction was quite small (1.8 cm/s).

Bridle tension and geometry

For the single haul in which both tension meters worked successfully, the bridle tension, combined over both sides, did not change significantly when regressed on the warp offset (df=11, P=0.69). This result indicates that any distortion of the trawl due to the offset treatments was not sufficient to appreciably affect the combined tension and, therefore, the hydrodynamic and frictional drag of the net and the bridles. However, changing the relative length of the warps resulted in a progressive transfer of the tension to the shorter warp (Fig. 4). For example, based on the average combined bridle tension (3248 kg), when the difference in warp lengths was 11 m, the shorter warp carried 72% of the total net and bridle drag.

Headrope speed through the water

The velocity component perpendicular to the headrope (U) decreased with increasing warp offset, whereas the absolute value of the velocity tangential (velocities from the port side of the sensor are opposite in sign to velocities from the starboard side) to the headrope (V) at its

center increased (Fig. 5). We interpret this as indication that the speed sensor at the headrope was rotated in relation to the direction of travel as the warp offset was increased. Calculating the angle between the perpendicular at the center of the headrope and the direction of travel as $\tan^{-1}(U/V)$, the angle increased from 11° at 3 m offset to 61° at 20 m offset. Although the absolute value of the tangential velocity was measured at values >0 at zero offset, the tangential velocity was not significantly different than zero (*t*-test, $P=0.71$). This result indicates that the alignment of the experimental tows in relation to the prevailing current was sufficient to reduce the cross current to negligible levels.

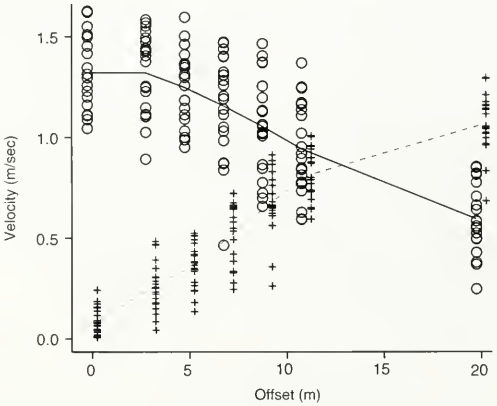

Figure 5

Current velocity (in m/sec) measured at the center of the headrope for each tow is shown separated into the component perpendicular to the headrope (O) and the component tangential to the headrope (+). The solid and dashed lines connect the means at each offset increment. Note, for clarity, that the offsets are incremented by plus or minus 0.1 m for the tangential and perpendicular components.

Net and door measurements

At zero offset, the mean door spread obtained was 61.9 m. The mean wing spread was 17.1 m, and the mean headrope height was 2.0 m. Differences in the means of all three quantities were not apparent at lower offsets, however headrope height and wing spread were more sensitive to changes in large offsets because both were significantly ($P<0.05$) greater than the zero offset means when offset was increased to 11 m, whereas door spread did not differ significantly until the offset was approximately 14 m (Fig. 6).

Bridle and footrope distance off-bottom by position

Bridle and footrope off-bottom distance varied considerably with position, not only with respect to the mean value but also with respect to the sensitivity of the mean to changes in offset. At zero offset, the mean off-bottom distance of the bridle declined from 12.3 cm at 50 m from the wing tips, to 3.2 cm at 40 m and 2.0 cm at 25 m (Fig. 7). Mean off-bottom distance remained small along the footrope, varying from 1.7 cm at 1 m behind the wing tip to 2.5 cm at the corner and 1.9 cm at the center.

The mean response to changes in offset varied greatly by position. Along the bridles, the most sensitive location was at 50 m, where off-bottom distance increased on the short side and decreased on the long side with increasing offset (Fig. 7). At 40 m, a similar pattern was repeated, but for most offsets on the long side, the off-bottom distance was near the minimum recorded, indicating that the bridle was resting on the bottom. At 25 m, the bridle was nearly always in contact with the bottom and off-bottom distance was insensitive to variations in warp offset. Along the footrope, the most sensitive position was the corner where off-bottom distance increased greatly with offset, particularly with positive offsets due to the relaxation in warp tension. At the center of the footrope, off-bottom distance was also sensitive to warp offset, responding almost identically on the long and short sides. At 1 m behind the wing tip, sensitivity to warp offset was quite low and the off-bottom distance indicated that the footrope was in contact with the bottom except for large offsets on the long side.

An alternate method of assessing the sensitivity of geometry of the 83-112 Eastern trawl to changes in offset is to determine if the mean off-bottom distance at 7 m, the maximum offset allowed under the NOAA protocols for the 83-112 Eastern trawl, differs statistically from the mean off-bottom distance at zero offset. Based on the bootstrapped confidence intervals (Fig. 7), off-bottom distance is significantly different from what it is at zero offset at the 50-m and 40-m bridle positions and at the center and corner footrope positions but is not significantly different at the wing and the 25-m bridle position.

Bridle shape and herding area

To understand better how the change in tension that accompanies offsets in warp leads to changes in bridle shape, we show the mean off-bottom distances plotted against the BCS positions on the wing and bridles for both the short side and long side of the trawl. From this perspective it is clear that as the tension is increased, off-bottom distance increases on the forward part of the bridle. Likewise, as the tension is reduced, the off-bottom distance decreases (Fig. 8). For flatfish, the effect of these changes in off-bottom distance is a change in the area subjected to herding stimuli. For the case where the reaction height is 1 cm, the bridle contact length is determined by the intersection of the line depicting

the reaction height with the lines depicting the bridle shape at each offset (Fig. 8). The change in these lengths on the short and long sides of the trawl is asymmetric with changes in warp offset (Fig 9). For the long side, bridle contact length increases linearly with positive offset. However, for the short side, bridle contact length decreases nonlinearly with warp offset—the greatest changes occurring with small offsets. This difference likely leads to a change in the total width of the herding area with changes in warp offset. If, for example, it is assumed that the angle-of-attack (α) is the same for the long and short sides of the trawl, then the width of the herded area declines to a minimum at about 8 m offset, at which the herded area is reduced by 10.3% compared to that at zero offset.

Headrope shape and effective net width

With increasing difference in warp length, the model we used to describe headrope shape predicts three distinct changes in shape. First, the headrope is distorted so that the wing tip on the short side of the trawl precedes that on the long side in the direction of travel (Fig. 10). The difference in the forward position of the wing tips, however, is much less than the warp offset. For example, an 11-m difference in warp length resulted in an offset in the position of the wing tips of only 2–3 m. This difference occurs because the increased tension on the short warp changes the catenary in both the bridles and the warps (i.e., both become effectively longer as the sag is reduced). Second, the headrope is distorted so that its center is increasingly displaced away from the midpoint between wings and toward the short side of the trawl. When this displacement occurs, the perpendicular at the center of the headrope is no longer aligned with the direction of travel. Third, the headrope is distorted so that the effective width of the net (i.e., the wing spread projected to the line perpendicular to the towing direction) becomes increasingly shorter than the distance measured by the acoustic net sensors. The difference between the effective and the measured net width is negligible for offsets up to 7 m but rapidly increases at greater offsets (Fig. 11).

Footrope shape viewed from in front of the net

The distance of the footrope off-bottom, when viewed from a position in front of the net, increases with increasing offset; however, the location of the maximum off-bottom distance in relation to the midpoint between wings, shifts slightly with increasing offset (Fig. 12). With offsets of 9 m or less, the position of maximum off-bottom distance is at the corner of the footrope on the long side of the trawl. However, with increasing offset, the shift in the position of the footrope corner changes because of the rotation of the trawl in relation to the direction of travel; and at a 20-m offset the footrope corner on the long side of the trawl is positioned, when viewed on a plane perpendicular to the direction of travel, almost exactly midway between the wing tips.

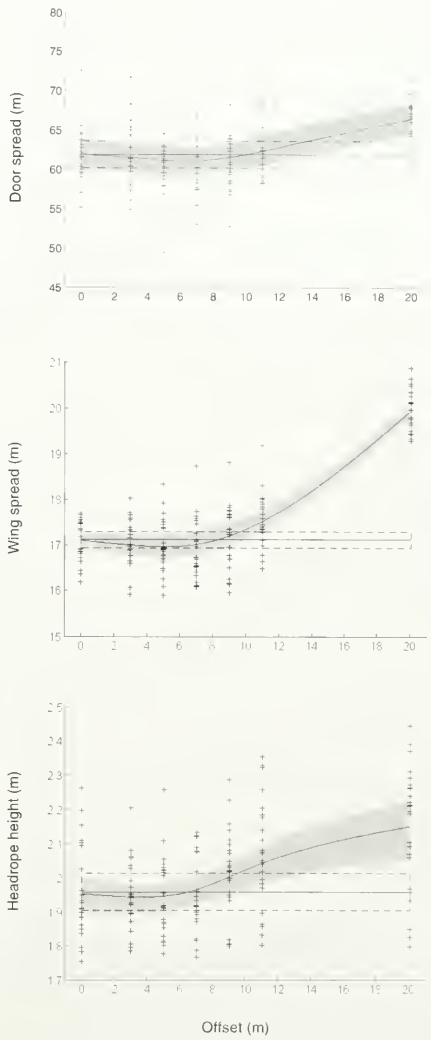

Figure 6

Mean door spread, wing spread, and headrope height are shown (+) plotted against offset increment. The means for all values of offset increment were fitted with a cubic spline function (solid curve). Bootstrapped 95% confidence bounds are shown with shading. Also shown are the mean door spread, wing spread, and headrope height for treatments with zero offset (solid horizontal line) and the corresponding bootstrapped 95% confidence bounds (dashed horizontal lines).

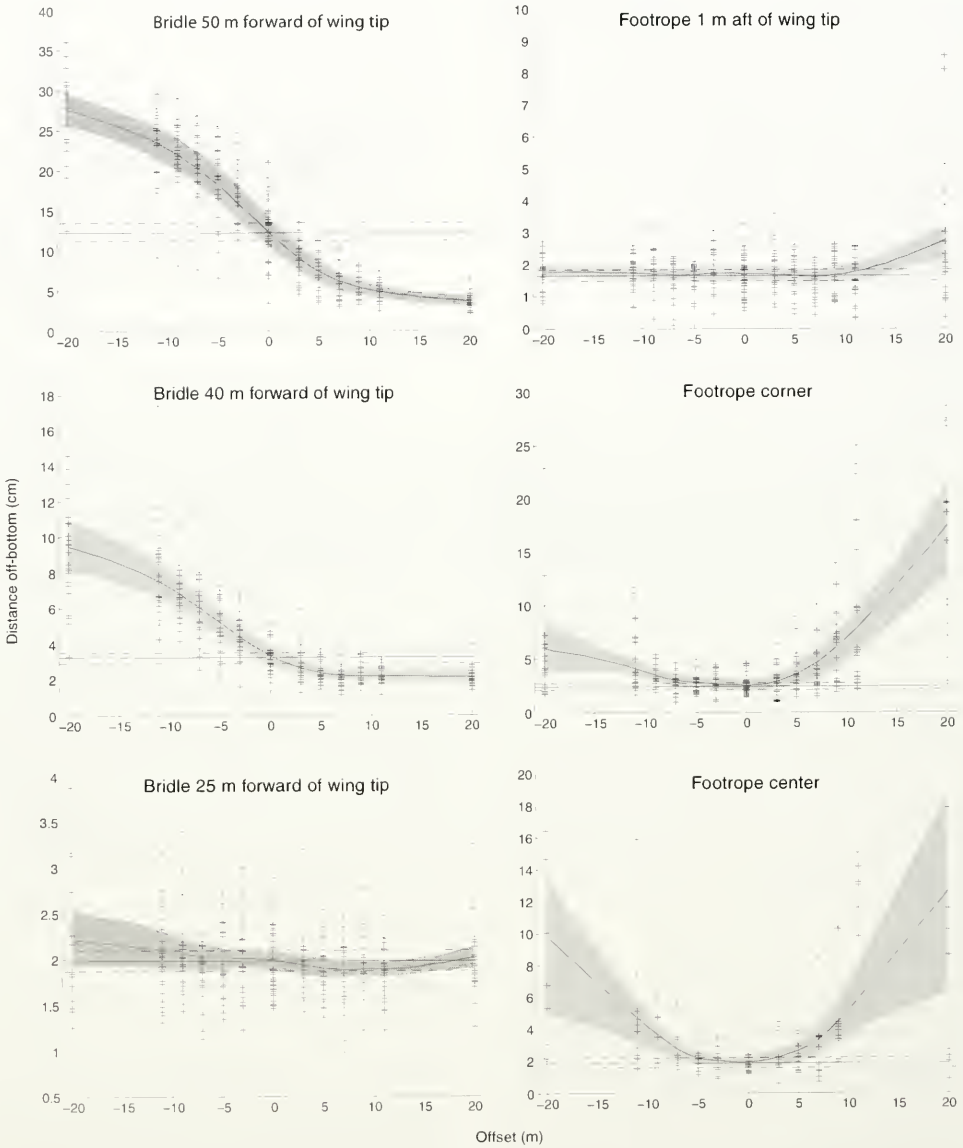

Figure 7

Mean bridle and footrope distance at each bottom contact sensor position is shown (+) plotted against offset increment. The means for all values of offset increment were fitted with a cubic spline function (solid curve). Bootstrapped 95% confidence bounds are shown with shading. Also shown is the mean distance off-bottom for only treatments with zero offset (solid horizontal line) and the bootstrapped 95% confidence bounds (dashed horizontal lines).

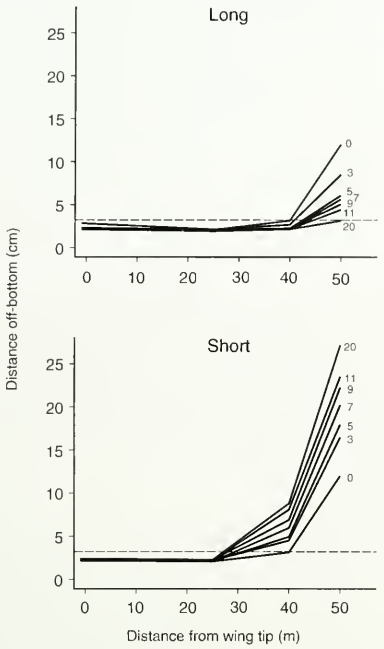

Figure 8

Mean off-bottom distance is shown plotted against the distance measured from the wing tip to the positions of the wing and the three bridle bottom contact sensors. This approximation to the shape of the bridle when viewed laterally is shown for each of the offset increments for both the side with the longer warp and the side with the shorter warp. The dashed line represents the hypothetical reaction height of a fish. The intersection of the dashed line with the solid line for each configuration defines the bridle length that is sufficiently close to the bottom to elicit a herding response.

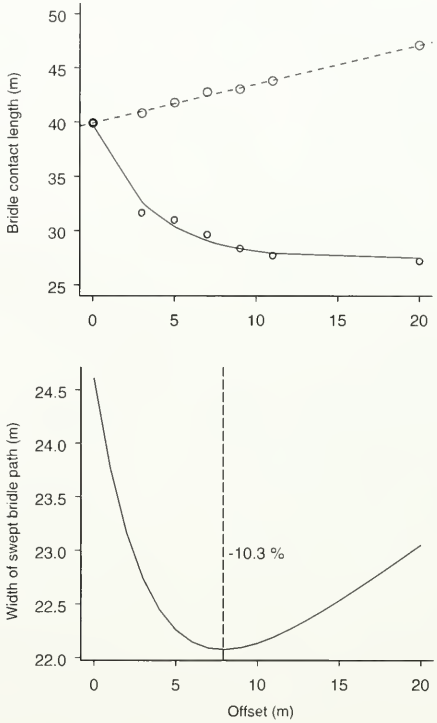

Figure 9

The length of the bridle with the off-bottom distance <1 cm is shown plotted against the offset increment in meters for both the short warp (solid line) and long warp (dashed line) sides of the trawl (upper panel). In both cases the lines are represented using cubic spline smoothing functions. The width of the swept bridle path as a function of warp offset is represented in the lower panel.

Discussion

There are two distinct approaches for judging whether a difference in warp length between the sides of a survey trawl will lead to a significant bias in estimates of relative abundance. In both approaches we focused on the adequacy of the maximum 7-m offset allowed for the 83-112 Eastern trawl under NOAA trawl survey protocols. In the first approach, we simply asked whether, given the sampling effort used in the experiment, any of the measured dimensions at 7-m offset were statistically different from zero offset. In our experiment, none of the three standard measures of trawl geometry (i.e., door spread, wing spread, and headrope height) differed from mean values at zero offset. This finding indicates that either these dimensions are fairly robust to changes in warp offset or that the acoustic measurement of these dimensions was insufficiently precise to detect a difference. Off-bottom distance, however, was significantly different at the two forward positions on the bridles and along the footrope at the center and corner positions.

From the perspective of trawl survey standardization, however, the detectability of changes in geometry is not of primary importance; these changes, however, may produce a significant effect on estimates of relative abundance. Bias in these estimates could result either because the change in trawl geometry leads to an inac-

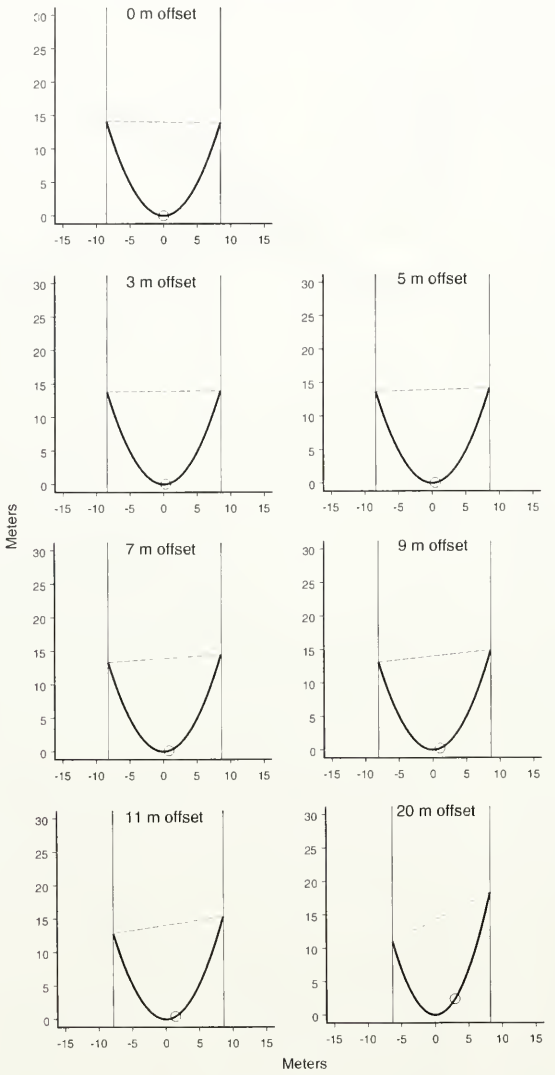

Figure 10

Estimated net shape (curve) and position of headrope center (O) at varying levels of warp offset. The mean distance between wing tips that was acoustically measured during the experimental tows is indicated with a dashed line. The maximum lateral dimensions of the net are indicated with solid vertical lines. The distance between these lines is the effective net width needed for estimating the area swept by the net.

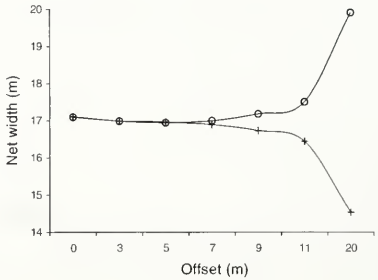

Figure 11

The mean distance between wing tips measured acoustically (O) during the experimental tows (net width) and the calculated effective net width (+) are shown plotted against the offset increment in meters. Note that there is little difference between the two measures of net width until the offset increment is increased to 9 m.

curate measurement of swept area or because it leads to a change in catch efficiency.

Relative abundance indices produced for the eastern Bering Sea shelf survey are based on catch per area swept between the trawl wings. As the net distorts on account of differential warp length, the effective net width will become increasing less than the width that is acoustically measured during the survey. Thus, net width will become increasingly overestimated and relative abundance of fish species therefore will be underestimated. At 7-m offset, however, the measured net width differed from the effective net width by only 0.5%, and therefore this source of error is unlikely to contribute to bias in the swept area estimates. However, the difference between measured and effective net width increases rapidly at greater offsets and could present a problem if a less restrictive threshold value of offset were used.

Catch efficiency of the 83-112 Eastern trawl depends primarily on 1) herding by the bridles, doors, and the mud clouds they create; 2) the escapement under the footrope; and 3) the escapement through the mesh in the body of the net. The relative importance of these three processes, however, will vary for the major species groups that are targeted in the surveys. Gadoids (primarily walleye pollock [*Theragra chalcogramma*] and Pacific cod [*Gadus macrocephalus*] appear to have little or no herding response to the 83-112 Eastern trawl (Somerton, 2004) and rarely pass under the footrope (Somerton, unpubl. data). However, both Pa-

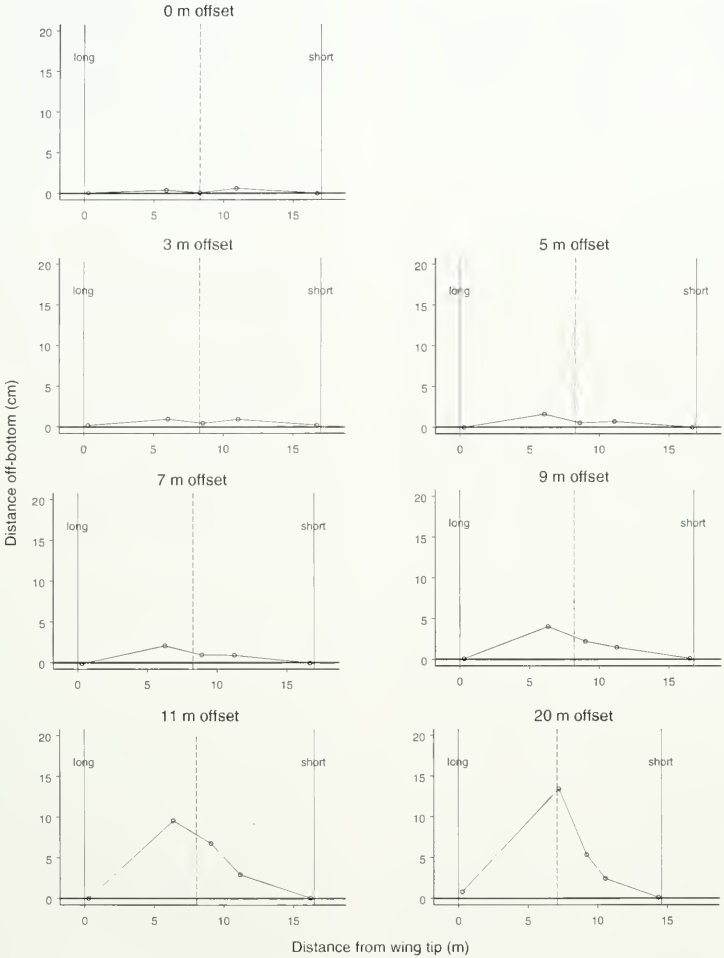

Figure 12

Mean off-bottom distances (in cm) at the five bottom contact sensor positions along the footrope (circles) are shown for each warp offset. The positions are projected onto the wing tip to wing tip plane to depict the footrope as it would appear if one were looking into the net from the direction of travel. The vertical solid lines indicate the positions of the wing tips on the long warp and short warp sides of the trawl. The dashed line indicates the midpoint between wing tips. Note that the projection considers the reduction in effective net width with increasing offset.

cific cod and walleye pollock are found gilled in the body of the net; therefore some mesh escapement may occur, especially if any distortion of the net results in altered water flow through the meshes. Video observations of crabs (snow and Tanner crabs [*Chionoecetes* sp.] and king crabs [*Paralithodes* sp.] show that they also exhibit little or no herding response to the 83-112 Eastern trawl (Weinberg, unpubl. data). However, both

Chionoecetes species (Somerton and Otto, 1999) and red king crab (Weinberg et al., 2004) do escape under the footrope. Flatfishes (including yellowfin sole [*Limanda aspera*], flathead sole [*Hippoglossoides elassodon*], and rock sole [*Lepidopsetta bilineata*] display a strong herding response to the 83-112 Eastern trawl (Somerton and Munro, 2001); as much as 49% of the catch consisted of fish that were herded by the bridles into the net path. Likewise, flatfishes are readily capable of escaping under the footrope and, for species such as yellowfin sole, at least 25% of the largest individuals escape in this manner (Munro and Somerton, 2002). Thus, the capture efficiency of the trawl is species-specific. The change in catch efficiency due to warp offset is likely minimal for species not captured as a function of herding and footrope escapement behaviors; however, because flatfish are susceptible to herding and are adept at footrope escapement, their catch rate could potentially be affected most by warp offsets.

Bridle efficiency (i.e., the fraction of fish in the area between the wing tips and doors that are herded into the path of the net) for flatfish catch is strongly influenced by the size of the herding area or area swept by the bridles because flatfish are stimulated to herd by the close approach or direct contact of the lower bridle. Although we were able to measure the off-bottom distance along the bridle and thereby predict the shape of the bridle, there is still considerable uncertainty as to the exact size of the herding area because the reaction height of a fish will vary with species, size, physiological state, state of arousal to the approaching bridle, viewing conditions for the fish, and, perhaps, other variables. Additionally, there is uncertainty in the estimate of the size of the herding area because it is based on the assumption of symmetry in the bridle angle-of-attack—a symmetry that is increasingly untenable with increasing offset. Despite this uncertainty, it is likely that the loss of herding area on one side of the trawl is not countered by an increase on the other side; thus some overall loss of herding efficiency is to be expected. In the hypothetical case chosen in our study, the reduction in herded area was 10.3%, which when applied to a strong herding flatfish such as rock sole (the herded component of the catch has been estimated to be about 49%, Somerton and Munro, 2001), the expected reduction in catch with an 8-m offset would be roughly 5%.

Flatfish escapement under the footrope will be influenced not only by the increase in off-bottom distance but also by the location along the footrope where the increase occurs. At a 7-m offset, the footrope off-bottom distance is about 2 cm higher in the footrope corner on the long side of the trawl and approximately 1 cm higher at the center and opposing corner than at zero offset (Fig. 12). Footrope off-bottom distances increased appreciably with greater offsets. Weinberg et al. (2002) demonstrated that flatfish escapement can increase with similar increases in footrope off-bottom distance; however their study focused on a different trawl and considered escapement for the entire footrope rather than by position along the footrope. Although we are unaware of any studies that quantify escapement rate by position along the footrope, our video observations indicate that flatfish are less likely to escape under the footrope near the wings than in the center (Somerton, unpubl. data). Because it is the center portion of the footrope where most of the increases in off-bottom distance occur in the 83-112 trawl, flatfish escapement is likely increased and potentially could represent a significant, but presently unquantifiable, loss in catch and a source of bias in estimates of relative abundance.

In conclusion, most aspects of the 83-112 Eastern trawl geometry were significantly degraded by warp offset differences equal to or greater than 7 m compared to zero offset. More importantly, the locations where the detectable differences occurred could affect catch efficiency; therefore a NOAA threshold value of 4% should be considered a maximum value for the 83-112 Eastern trawl and perhaps a more conservative value (less than 4%) would be prudent. However, given today's standardized survey procedures for measuring warp and for real-time monitoring of warp offset, the probability of warp offsets even approaching 7 m is highly unlikely on our surveys when locked-winches are used. Likewise, we argue that any appreciable differences in warp lengths between sides due to stretching are unrealistic because AFSC charter vessels use large diameter, compressed, solid-core wire. In fact, a review of the 413 hauls made during the 2004 EBS survey revealed that only three tows had a recorded maximum 1-m length difference between sides (Weinberg, unpubl. data).

Acknowledgments

We would like to thank Captain Brad Lougheed and the FV *Vesteraalen* crew, Niles Griffen, Waldemar Janezak, Van Ngo, and Todd Becker for their outstanding professionalism, positive attitudes, and constant attention to detail; AFSC scientists Stan Kotwicki and Dennis Benjamin for their assistance at sea; reviewers Guy Fleischer and Henry Milliken for their helpful comments; and the AFSC editorial staff, including Gary Duker, Jim Lee, and Karna McKinney for their help during the in-house review and manuscript preparation process.

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Appendix 1: Estimating headrope and footrope shape when the warps differ in length

If a trawl headrope has the same shape as a flexible twine under a uniformly distributed load, then the shape of the headrope can be approximated as a quadratic (parabolic) function (Fridman, 1969; p. 84) as

$$y = cx^2, \tag{1}$$

where c is a constant controlling the shape (Fig. A1). As the headrope is distorted by a differential in warp length, not only does the value of c change, but the headrope is displaced along the path of the parabola, so that its center is no longer aligned with the vertex of the parabola. A unique solution to the shape of the headrope when it is distorted in this manner can be determined from three types of data: the total headrope length (L), the measured distance between the wing tips (W), and the measured slope (tangent) of the parabola at the center of the headrope (tan). The third quantity can be obtained from the V (perpendicular to the footrope) and U (tangential to the footrope) velocities measured by the headrope speed sensor as the quotient U/V. With these quantities, the solution can be obtained as follows.

A small length interval measured along the headrope can be expressed as

$$ds = (dy^2 + dx^2)^{\frac{1}{2}}. \tag{2}$$

Which, after substitution of the derivative of Equation 1, is

$$ds = \left(1 + (2cx)^2\right)^{\frac{1}{2}} dx. \tag{3}$$

The length of any segment of the headrope, measured from the port end (x_{lower}), is then

$$S = \int_{x_{lower}}^{x} \left(1 + (2cx)^2\right)^{\frac{1}{2}} ds. \tag{4}$$

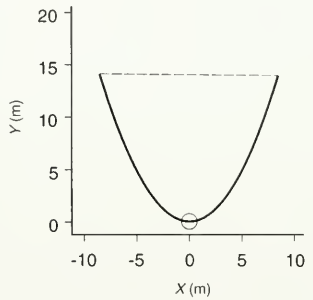

Figure A1

Shape of a trawl headrope as described by a parabola. The total length of the headrope (shown with a solid line) is equal to L. The measured width of the trawl (shown with a dashed line) is equal to W. The circle indicates the center of the headrope where a speed sensor is located. The speed sensor measures water speed both perpendicular and parallel to the headrope.

A segment equal to the total length of the headrope is obtained by integrating up to the starboard end (x_{upper}).

The solution is approximated numerically in two stages. First, for a trial value of c, Equation 4 is integrated from trial values of x_{lower} up to the value of x at which S=L/2 (i.e., x_{middle}). The tangent at this position is then evaluated as $2cx_{middle}$ (based on the derivative of Eq. 1). This process is then repeated iteratively to find the value of x_{lower} for the specified value of c at which the calculated tangent equals the tangent value determined from the headrope speed sensor. The value of x_{upper} is

then determined by integrating Equation 4 from x_{lower} to the value of x at which $S=L$. The wing tip to wing tip distance $D_{wingtip}$ is then calculated as

$$D_{wingtip} = \left((y_{upper} - y_{lower})^2 + (x_{upper} - x_{lower})^2\right)^{\frac{1}{2}}, \quad (5)$$

where y_{upper} and y_{lower} are obtained from Equation 1. In the second stage, c is varied and the above process is repeated iteratively until the value of $D_{wingtip}$ is found that is closest to the measured net spread. At this point the calculated values of $D_{wingtip}$ and the tangent at the headrope center will equal the measured values.

The headrope-shape model for each offset was used to project the off-bottom distances measured at the five positions along the footrope onto a plane orientated perpendicular to the direction of travel to depict the shape of the footrope as it would appear from a position in front of the trawl. To do this, a shape function was developed for the footrope. Assuming that the coordinates of the endpoints of the footrope (x_{lower}, x_{upper}, y_{lower}, y_{upper}) were the same as the headrope, Equation 5 was iteratively integrated with varying values of c until the estimated value of the footrope length (S) equaled the true length (34.1 m):

$$S = \int_{x_{lower}}^{x_{upper}} \left(1+(2cx)^2\right)^{\frac{1}{2}} dx. \quad (6)$$

Once c is determined, Equation 4 is integrated to find the value of x associated with the value of S at each BCS (bottom current sensor) position on the footrope.

The effect of autotrawl systems on the performance of a survey trawl

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Abstract—Three aspects of a survey bottom trawl performance—1) trawl geometry (i.e., net spread, door spread, and headrope height); 2) footrope distance off-bottom; and 3) bridle distance off-bottom—were compared among hauls by using either of two autotrawl systems (equal tension and net symmetry) and hauls conducted with towing cables of equal length and locked winches. The effects of environmental conditions, vessel heave, crabbing (i.e., the difference between vessel heading and actual vessel course over ground), and bottom current on trawl performance with three trawling modes were investigated. Means and standard deviations of trawl geometry measures were not significantly different between autotrawl and locked-winch systems. Bottom trawls performed better with either autotrawl system as compared to trawling with locked winches by reducing the variance and increasing the symmetry of the footrope contact with the bottom. The equal tension autotrawl system was most effective in counteracting effects of environmental conditions on footrope bottom contact. Footrope bottom contact was most influenced by environmental conditions during tows with locked winches. Both of the autotrawl systems also reduced the variance and increased the symmetry of bridle bottom contact.

Autotrawl systems proved to be effective in decreasing the effects of environmental factors on some aspects of trawl performance and, as a result, have the potential to reduce among-haul variance in catchability of survey trawls. Therefore, by incorporating an autotrawl system into standard survey procedures, precision of survey estimates of relative abundance may be improved.

Manuscript submitted 27 October 2004 to the Scientific Editor's Office.

Manuscript approved for publication 6 June 2005 by the Scientific Editor.

Fish. Bull. 104:35–45 (2006).

Bottom trawl survey operating procedures are standardized in order to reduce the variability of catch per unit of effort (CPUE) estimates. Many of the current standardization procedures address the efficiency of the trawl gear and the maintenance of constant catchability among samples and over time. Despite these efforts, variability in trawl catchability can be exacerbated by uncontrollable environmental conditions. Variables such as surface and bottom currents, sea state, wind direction, varying substrate types and inclinations, and depth of tow may all contribute to differences in gear efficiency by influencing the area swept by the net (Rose and Nunnallee, 1998), the herding efficiency of the bridles (Somerton and Munro, 2001; Somerton, 2003), and escapement beneath the footrope (Weinberg et al., 2002).

Many bottom trawl surveys conducted by the National Marine Fisheries Service, such as the Alaska Fisheries Science Center's (AFSC) eastern Bering Sea (EBS) shelf survey, operate with trawl winch brakes, set or locked, and tows are made with equal amounts of towing cable (warp) on both sides of the vessel. Other than by controlling towing speed and direction, these surveys are unable to compensate for changing environmental conditions. In contrast, autotrawl systems are widely used by the commercial fleet and are purported to improve fishing performance by stabilizing trawl geometry over varying environmental conditions, such as rough weather when vessel heave produces an upward lift on the trawl door resulting in loss of ground shear and wing spread, or over rough bottom when doors and nets have a greater probability of snagging. If autotrawl systems are able to reduce some of the variability in gear efficiency that is due to environmental variability, such as sea state and currents, then including the use of autotrawl systems as a standard survey bottom trawl procedure may improve the precision of survey results.

In simple terms, autotrawls are dynamic systems that operate on the principle of ensuring that the trawl is being towed in a direction perpendicular to the center of the footrope and headrope in order to optimize its performance. We are aware of two styles of autotrawl systems currently marketed. The first is a tension-controlled system that reacts to the difference in warp tension between winches by equalizing hydraulic pressure (equal tension). When the tension on either side exceeds that of the other side (a user-defined threshold) due to factors such as increased drag, currents, sediments, or steep slopes, the system lengthens that warp to equalize the pressure between the two winches. Conversely, when the tension decreases on one warp, the system compensates by shortening that warp to equalize pressure between the two winches. The second autotrawl style is a symmetry-controlled system that actively adjusts warp length in response to cross flow

signals from a sensor mounted on the trawl headrope. This system operates on the principle that net skewing can be caused by a crosscurrent. If the net is pulled square to the direction of flow then, its geometry will be symmetrical and trawl performance will be optimized.

In the late summer of 2003, the AFSC conducted an experiment to examine the effect of these two types of autotrawl systems on the geometry of a survey trawl, comparing them to towing with equal amounts of warp on each side with the winches locked. The study considers three aspects of trawl performance: 1) the factors of trawl geometry influencing the area and volume swept by the trawl (door spread, wing spread, and headrope height); 2) the bottom-tending performance of the footrope; and 3) the bottom-tending performance of the lower bridles.

Materials and methods

Operations and instrumentation

The experiment was conducted during 19–25 September 2003 aboard the chartered 38-m-long commercial stern trawler FV *Vesteraalen* on smooth, relatively level bottom in 115 m of water at a site approximately 70 km north of Unimak Pass in the Bering Sea (55°10′N, 166°15′W). The *Vesteraalen* is powered by a single 1725-hp engine and is equipped with split Rapp Hydema (Rapp Hydema AS, Bodø, Norway) trawl winches carrying 2.5 cm (1″) diameter, compacted, solid-core trawl warp. The winches are controlled by a Scantrol 2000 (Scantrol, Bergen, Norway) winch control system capable of quickly switching to different towing modes as requested by the vessel operator. For this experiment towing was performed with the codend open and with three different winch control modes: locked winches with equal amounts of warp on the port and starboard side (locked); a tension-controlled autotrawl, which maintains equal tension on both warps by adjusting warp length based on the drag forces on each side (tension); and a symmetry-controlled autotrawl, which adjusts warp length according to side current forces in order to "optimize" water flow through the net (symmetry). The symmetry-controlled system requires a real-time speed sensor capable of detecting the direction of water flow across the headrope. We used an acoustically linked Scanmar (Scanmar, Asgardstrand, Norway) trawlspeed sensor that transmits flow data at 24-sec intervals both perpendicular and tangential to the headrope at its center. For this experiment and when in symmetry mode, the Scantrol system adjusted warp length at 30-sec intervals in response to changes in tangential velocity.

The experiment was conducted with the AFSC standardized trawl for the EBS shelf survey, the 83-112 Eastern bottom trawl. The 83-112 Eastern is a low-rise, 2-seam flatfish trawl designed to fish on smooth, soft bottom. The nylon net is constructed of 10.1-cm stretch mesh in the wing and body, 8.9-cm mesh in the intermediate, and double 8.9-cm mesh lined with 3.1-cm mesh in the codend. It is towed behind a pair of 1.8×2.7 m steel "V" doors, weighing approximately 816 kg apiece, which are attached to the net by two 3-m-long, 1.6-cm long-link chain door legs, a 12.2-m-long, 1.9-cm diameter stranded-wire door leg extension, and a pair of 55-m-long, 1.6-cm diameter bare stranded-wire bridles on each side (Fig. 1). The 25.5-m-long (83 feet) headrope has forty-one evenly spaced, 20.3-cm diameter floats providing 116.4 kg of total lift. The 34.1-m-long (112 feet), 5.2-cm diameter footrope is constructed of 1.6-cm diameter stranded-wire rope that is protected with a single wrap of both 1.3-cm diameter polypropylene line and split rubber hose. The footrope is weighted with 51.8 m of chain (0.8-cm proof-coil) attached at every tenth link, forming 168 loops to which the netting is hung. An additional 0.6-m-long, 1.3-cm long-link chain extension connects each lower bridle to the trawl wing tips to help keep the footrope close to the bottom.

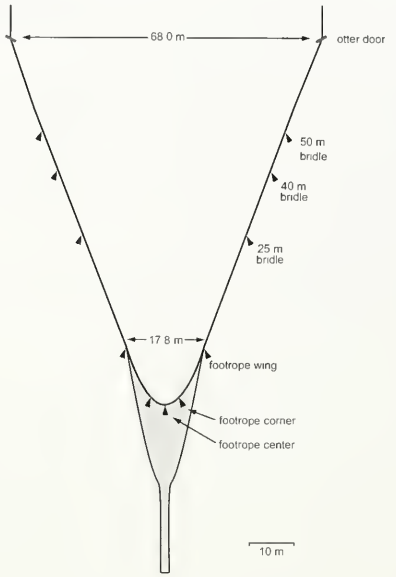

Figure 1

Schematic diagram of the 83-112 Eastern bottom trawl and rigging shown from above. Mean door spread (68.0 m) and mean wing spread (17.8 m) were calculated from experimental tows made at a depth of 115 m with the winches locked and 366 m of trawl warp out on each side. Bottom contact sensor units, shown as oversized triangles along the bridle and footrope, are labeled by position, as discussed in the text.

Prior to experimental towing, trawl warps were measured and marked at 366 m, the amount of warp used on the EBS survey when stations are fished at a depth of 115 m, the depth of our study site. Warps were measured and marked in accordance with AFSC protocol (Stauffer, 2004) by using in-line wire counters (Olympic 750-N, Vashon, WA) while at the same time, calibration of the geometric winch counters associated with the autotrawl system was performed.

A haul consisted of towing at a vessel speed of 3 knots while steering a steady course over ground. Tow direction was selected by attempting to expose the trawl to the maximum amount of side current. Vessel speed and position were measured at 2-sec intervals with satellite navigation. Each haul consisted of two treatment sets in which three 15-min towing treatments (locked winches [locked], tension-controlled autotrawl [tension], symmetry-controlled autotrawl [symmetry]) were conducted, allowing at least two minutes between treatments for the net to equilibrate. Randomizing the order of treatments within each treatment set reduced the influence of treatment order on trawl performance introduced by sea state, wind, and tidal currents. Likewise, towing at the same site for the duration of the experiment eliminated bias that could be attributed to varying substrate.

Wing spread, door spread, and headrope height were measured acoustically with Scanmar sensors at 4-sec intervals to the nearest 0.1 m. Footrope distance from the sea floor (cm) was measured at 0.5-sec intervals and averaged over 1.5-sec periods at five positions along the footrope simultaneously by placing bottom contact sensors (BCS) at the center, at both trawl corners (located 3 m to either side of the center), and on each wing 1 m aft of the wing tips (Fig. 1). These sensors are self-contained units consisting of a tilt meter capable of measuring angle to the nearest 0.5° and a data logger housed in a watertight stainless steel container that fits inside a steel sled (Somerton and Weinberg, 2001). One side of the sled clips into a clamp that pivots freely on the trawl footrope and the other end drags along the bottom (Fig. 2). Changes in the distance of the footrope from the bottom produce changes in the recorded tilt angle. Conversion from tilt angle to distance off-bottom was accomplished with a calibration function determined for each BCS unit by fitting a quadratic function to data derived from a separate calibration experiment in which tilt angles were recorded when the footrope clamp was elevated set distances from a hard surface. The BCS unit extended out from the footrope 44 cm and its combined weight (consisting of BCS, sled, and footrope clamp) was 8.9 kg in seawater. The thickness of the clamp beneath the footrope was 2 cm. Because underwater video equipment was unavailable for this experiment, the extent to which this clamp penetrates into variable substrates was not estimated.

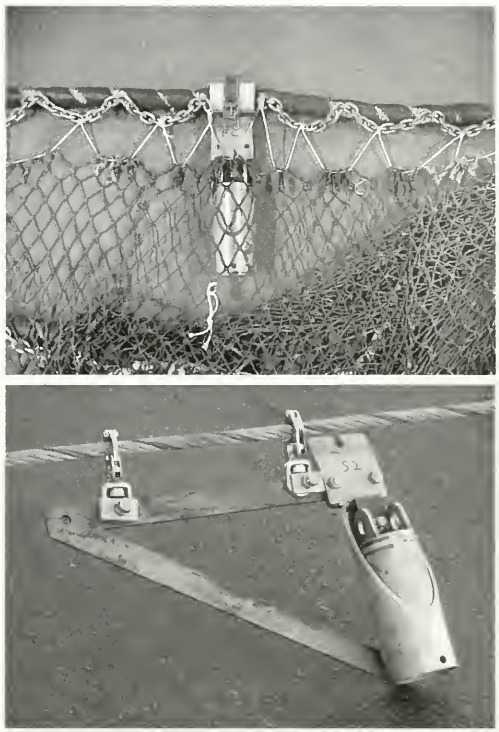

Figure 2

Bottom contact sensors mounted to the footrope (top) and the bridle (bottom).

Bridle distance from the bottom was measured at three positions simultaneously on both port and starboard sides by placing BCS units 25, 40, and 50 m forward of each wing tip. The BCS units and sled were mounted on triangular frames designed to hold them perpendicular to the bridle (Fig. 2, Somerton, 2003). The triangular frame measured 49 cm in its longest dimension. The combined weight of a BCS unit and frame was 8.7 kg in seawater.

In addition to trawl mensuration, data were also collected on certain environmental variables during the different towing modes. Three variables were studied: 1) vessel heave measured at the trawl block; 2) the relative degree of offset of the warps from the heading of the vessel (crabbing); and 3) bottom current velocity both parallel and perpendicular to the direction of the vessel.

The effect of sea state on the vertical displacement and attitude of the vessel is transmitted to the footrope from the trawl blocks through the trawl warps and

likely causes variable bridle and footrope contact with the bottom. Vessel heave at the starboard trawl block was used as a proxy for sea state. Heave, pitch, and roll data were collected at 1-sec intervals with a heave sensor (VT TSS, DMS-25, Watford, UK) mounted in the bridge along the centerline of the vessel. Heave data at the starboard block were then predicted, given the x, y, z coordinates of the block from the heave sensor, as distance (cm) from its equilibrium position. In the analyses, the standard deviation of the heave was used as the index of sea state.

Net crabbing was subjectively assessed on a four-point scale by a single observer, then numerically coded as follows; 1) none—the net trailed straight behind the vessel; 2) slight—the warp could be seen entering the water between the side rail and the aft gantry; 3) moderate—the point of entry of the warp into the water was blocked from view by the aft gantry; and 4) severe—the warp was observed entering the water behind the stern ramp. Conditions usually remained constant and one observation was made per towing-mode treatment. However, in some instances conditions changed rapidly and warranted more than one code. In such cases the average of the observation codes was used in the analyses.

Bottom current direction and velocity (cm/sec) were measured at 10-sec intervals with an oceanographic current meter (Nobska, MAVS-3, Woods Hole, MA) moored in the vicinity of our trawling activity three meters from the bottom. The current data were partitioned into two directional components, one parallel to the course of the vessel and the other perpendicular, and averaged for each sample treatment.

Data analyses

Comparison of the means and standard deviations among treatments Our null hypothesis, that the three treatments had the same effect, was tested with a Kruskal-Wallis one-way ANOVA for all measures of trawl performance. We selected this test because of the skewed nature of the data. To describe the effect of the three treatments on trawl geometry features the mean and standard deviation (SD) were calculated for the wing spread, door spread, and headrope height off-bottom from each treatment in each haul.

To describe the bottom-tending performance of the footrope we calculated the following statistics for each treatment:

1 mean footrope distance off-bottom—the sum of mean distances off-bottom along the footrope, from five footrope BCS units;
2 standard deviation of the footrope distance off-bottom—the sum of standard deviations along the footrope, from five footrope BCS units; and
3 symmetry of the footrope distance off-bottom—the sum of the absolute difference between the means of the two wing positions and the absolute difference between the means of the two corner positions on the footrope.

To describe the bottom-tending performance of the lower bridle, we considered only the BCS unit positioned 40 m from the wing tip. The variability in bottom-tending performance of the bridles 40 m from the wing tip may have the highest impact on the catchability of the trawl because the BCS at the 25 m position was always on the bottom and the BCS at the 50 m position was always off the bottom. Performance of the bridles at the 40 m position was characterized by

1 mean bridle distance off-bottom—the sum of the mean distances off-bottom from the BCS units located 40 m forward of the wing tip on both lower bridles;
2 standard deviation of the bridle distance off-bottom—the sum of the standard deviations from the BCS units located 40 m forward of the wing tip on both lower bridles; and
3 symmetry of the bridle distance off-bottom—the absolute difference between means from the BCS units located 40 m forward of the wing tip on both lower bridles.

Assessment of the effect of environmental factors If differences among towing mode treatments were found by the ANOVA ($P<0.05$), then the effects of heave, crabbing, and bottom current on gear performance within each treatment were explored. Multiple regression analyses were performed for each of the treatment statistics with environmental variables as dependents. At the start of the analyses, the models included all four dependent variables (heave, crabbing, current parallel, and current perpendicular to the tow direction). Variance inflation factors (VIFs) were calculated for all variables to test for multicollinearity (Neter et al., 1996). Dependent variables in all models had VIFs ranging from 1 to 1.4, indicating that no serious multicollinearity existed among dependent variables. Models were simplified (backward deletion) until all P-values of the individual slopes were lower than 0.05. This procedure enabled us to establish which variables had a statistically significant impact on performance of the trawl within each treatment.

Results

A total of 21 successful hauls were performed during the experiment, yielding 42 possible treatment sets for analyses. The number of successful treatment sets included in the analyses varied for each of our performance statistics as a result of either malfunctions or poor survey trawl performance caused by conflicts with abandoned fishing gear.

Comparison of the means and standard deviations among treatments

Trawl geometry A total of 41 treatment sets were used to analyze the six trawl geometry statistics (means and

Table 1

Means of the trawl geometry statistics (m) and *P*-values of the Kruskal-Wallis test for differences between three towing-mode treatments. Locked=locked winches; symmetry=symmetry-controlled autotrawl; and tension=tension-controlled autotrawl.

Statistic		Locked	Symmetry	Tension	*P*-value
Wing	mean	17.76	17.77	17.85	0.6952
	SD	0.69	0.70	0.73	0.9157
Door	mean	68.03	67.67	67.71	0.8380
	SD	1.87	1.73	2.14	0.0977
Height	mean	1.82	1.81	1.81	0.7618
	SD	0.21	0.20	0.20	0.8618

Table 2

Means of the footrope and bridle statistics (cm) and *P*-values of the Kruskal-Wallis test for differences between three towing-mode treatments. Locked=locked winches; symmetry=symmetry-controlled autotrawl; and tension=tension-controlled autotrawl.

Statistic		Locked	Symmetry	Tension	*P*-value
Footrope	mean	13.98	13.09	12.08	0.0441
	SD	6.39	5.67	5.24	0.0391
	symmetry	1.95	1.44	1.45	0.0554
Bridle	mean	7.50	6.69	6.28	0.0286
	SD	4.91	4.03	3.37	0.0046
	symmetry	1.59	0.93	0.88	0.0030

standard deviations of the wing spread, door spread, and net height). No significant differences were detected among the three towing modes (Table 1); consequently, no environmental variables were tested for their influence on trawl geometry.

Footrope distance off-bottom Analyses based on 33 successful treatment sets produced varying results among the three measures describing the bottom tending performance of the footrope. Mean footrope distance off-bottom differed significantly among the three towing modes (Table 2, Fig. 3). Footrope distance was lowest for the tension treatment followed by the symmetry treatment and locked winches. The greatest observed difference occurred between the locked (13.98 cm) and the tension treatment (12.08 cm). Standard deviation in footrope distance off-bottom also differed significantly among treatments. Differences were similar to those observed for the mean, in that the lowest SD was observed for the tension treatment (5.24 cm) and the highest SD was observed for the locked treatment (6.39 cm). Because the variance equals the square of the standard deviation, this seemingly small reduction in standard deviation corresponds to a fairly large reduction in the variance (~30%). Symmetry in the footrope off-bottom distance did not differ significantly ($P=0.0554$) among the three towing modes.

Bridle distance off-bottom A total of 34 successful treatment sets were used to analyze the bridle distance off-bottom data. Mean bridle distance off-bottom differed significantly among treatments (Table 2, Fig. 4); it was lowest for the tension treatment (6.28 cm) and highest with the winches locked (7.50 cm). Standard deviation of bridle distance off-bottom also differed significantly among the three towing modes. SD values were significantly lower in the autotrawl towing modes, being lowest in the tension treatment (3.37 cm) and highest in the locked treatment (4.91 cm). Bridle distance off-bottom was most symmetrical in the symmetry and tension towing modes. Symmetry and tension means were similar (0.93 cm and 0.88 cm, respectively) and significantly lower than that observed for the locked-winches treatment (1.59 cm).

Assessment of the effect of environmental factors

Footrope distance off-bottom The effect of environmental factors on our three measures describing the bottom tending performance of the footrope produced varying results. Mean distance off-bottom was significantly affected by heave only, during all treatments (Table 3, Fig. 5). The standard deviation of the footrope distance off-bottom was also significantly affected by heave, crabbing, and bottom current parallel to the direction of the

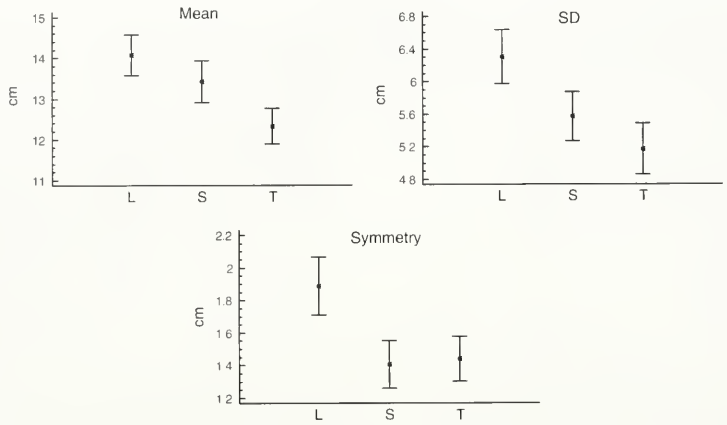

Figure 3

Means and standard errors of the footrope distance off-bottom, standard deviation of the footrope distance off-bottom, and footrope symmetry for the locked winches (L), symmetry (S), and tension (T) treatments.

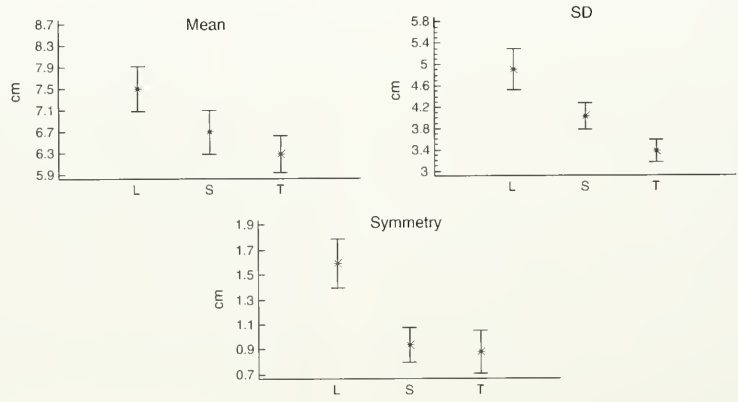

Figure 4

Means and standard errors of the bridle distance off-bottom, standard deviation of the bridle distance off-bottom, and bridle symmetry for the locked winches (L), symmetry (S), and tension (T) treatments.

tow during some treatments (Table 3, Fig. 6). Heave had a greater effect on footrope SD during the locked-winches treatment (slope=0.0610) than during the symmetry treatment (slope=0.0381). Similar effects were also detected for crabbing (slopes=1.2355 and 0.8493, respectively). Current speed in the direction of the tow affected footrope SD only during the symmetry mode. Heave, crabbing, and current velocity had no effect on

Table 3

Multiple regression model slope coefficients with P-value <0.05, for locked winches, symmetry-controlled, and tension-controlled towing modes (Y=bottom current parallel to the direction of the tow, Abs$X$=absolute value of the crosscurrent).

Statistic		Treatment	Heave	Crabbing	Y	Abs$X$	R^2	P-value
Footrope	mean	locked	0.0572	—	—	—	9.04	0.0495
		symmetry	0.0713	—	—	—	15.64	0.0227
		tension	0.0544	—	—	—	16.14	0.0205
	SD	locked	0.0610	1.2355	—	—	58.93	<0.0001
		symmetry	0.0381	0.8493	−0.0446	—	33.96	0.0066
		tension	—	—	—	—	—	>0.05
	symmetry	locked	—	—	0.0255	—	15.42	.0238
		symmetry	—	—	—	—	—	>0.05
		tension	—	—	—	—	—	>0.05
Bridle	mean	locked	0.0680	—	—	—	19.66	0.0086
		symmetry	—	—	—	—	—	>0.05
		tension	0.0491	—	—	—	14.88	0.0242
	SD	locked	0.0796	0.9536	—	—	60.30	<0.0001
		symmetry	—	—	—	—	—	>0.05
		tension	0.0411	0.3023	—	—	33.83	0.0017
	symmetry	locked	—	—	—	0.0556	26.58	0.0018
		symmetry	—	—	—	—	—	>0.05
		tension	—	—	—	0.0361	13.25	0.0343

footrope SD during the tension mode. The symmetry in footrope distance off-bottom was significantly affected by the current parallel to the direction of the tow during the locked-winches treatment only (Table 3, Fig. 7).

Bridle distance off-bottom Mean bridle distance off-bottom was affected by heave only during some of the treatments (Table 3, Fig. 8). Heave had a greater impact on the mean bridle distance off-bottom during the locked-winches treatment (slope=0.0680) than during the tension treatment (slope=0.0491). The standard deviation of the bridle distance off-bottom was affected by heave and crabbing during two of the treatments (Table 3, Fig. 9). Heave had an effect on the SD of the bridle distance off-bottom during both locked (slope=0.0796) and tension (slope=0.0411) treatments. A significant effect due to crabbing was also detected during these same two treatments (slopes 0.9536 and 0.3023, respectively). During the symmetry mode no effect due to any of the environmental conditions was detected, even though SD was almost always higher than that observed in the tension mode, with the exception of extreme heave conditions. Symmetry in the bridle distance off-bottom was affected only by crosscurrent (Table 3, Fig. 10). Crosscurrent had an effect on the symmetry during the locked (slope=0.0556) and tension (slope=0.0361) treatments.

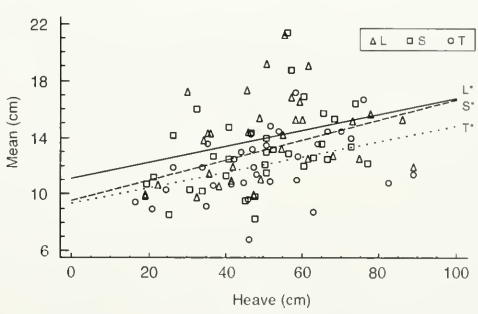

Figure 5

Comparison of regression lines illustrating the relationship between the mean footrope distance off-bottom and heave for locked winches (L), symmetry (S), and tension (T) treatments. Treatments in which heave had a statistically significant effect on the mean are identified with an asterisk (*).

Discussion

The objective of this study was to identify towing modes that could potentially reduce variance in the catchability of the 83-112 Eastern bottom trawl among hauls. Three separate aspects of trawl performance affecting catchability were investigated: trawl geometry, bottom tend-

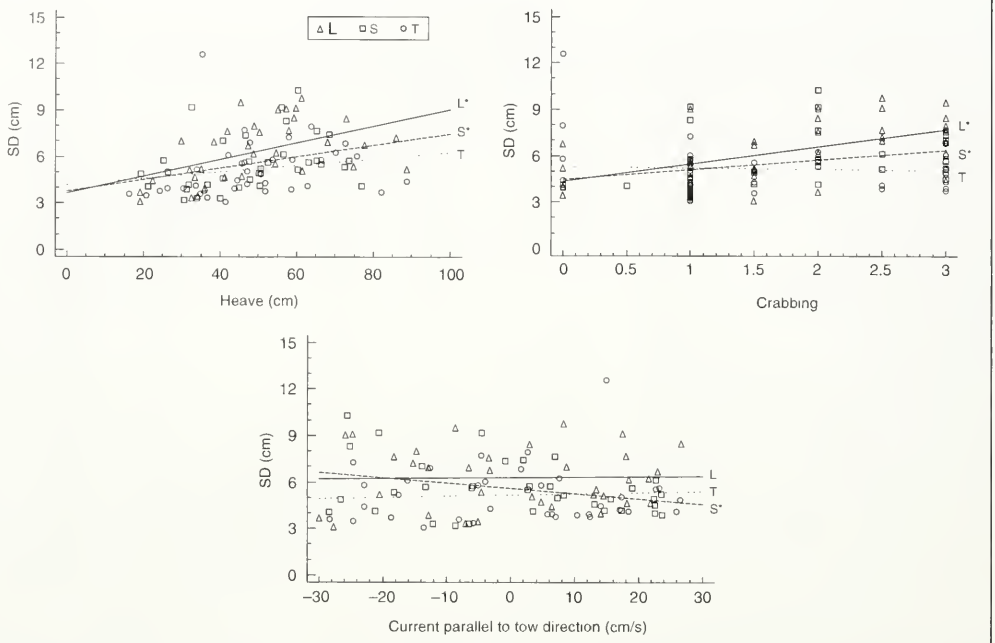

Figure 6

Comparison of regression lines illustrating the relationship between the standard deviation (SD) of the footrope distance off-bottom and environmental variables for locked winches (L), symmetry (S), and tension (T) treatments. Treatments in which the environmental variable had a statistically significant effect on the SD are identified with an asterisk (*).

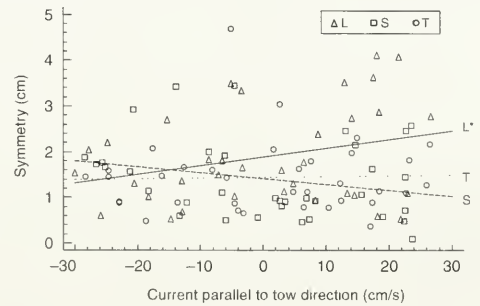

Figure 7

Comparison of regression lines illustrating the relationship between the symmetry of the footrope distance off-bottom and current parallel to the direction of the tow for locked winches (L), symmetry (S), and tension (T) treatments. Treatments in which the current had a statistically significant effect on the symmetry are identified with an asterisk (*).

ing performance of the footrope, and bottom-tending performance of the lower bridles.

Trawl geometry

Because wing and door spread and net height variability all influence catchability of a trawl (Rose and Nunnallee, 1998), surveys would stand to benefit from autotrawl systems if variances in the trawl geometry features were reduced. Our study showed that neither autotrawl system improved trawl geometry over the conventional locked-winches towing mode.

Footrope

Previous studies have demonstrated that escapement under the footrope is an important factor determining the catchability of the 83-112 Eastern survey trawl (Somerton and Otto 1999; Munro and Somerton, 2002; Weinberg et al., 2004). Periodic separation between the footrope and the bottom contribute to variability in catchability and have

been shown to be influenced by a variety of factors, such as net speed through the water (Somerton and Weinberg, 2001) that can increase footrope distances off-bottom. Weinberg et al. (2002), using a different survey bottom trawl, found capture probability of some benthic species to decrease as a result of footrope separations with the bottom. These findings likely apply to the 83-112 Eastern trawl as well. Because capture probability is generally size dependent (Munro and Somerton, 2002), an unstable footrope may not only increase the variance of overall biomass estimates, but may bias the size distribution data generated by a survey as well. If autotrawl systems can help maintain footrope contact with the bottom, then the use of an autotrawl during surveys may be warranted.

In our experiment, the tension-controlled autotrawl system provided the best footrope contact overall and the lowest standard deviation (Fig 3). High heave and moderate to strong crabbing were largely responsible for the differences observed in the bottom-tending performance of the footrope among treatments (Figs. 5–7). The tension treatment was most effective in counteracting the effects of environmental conditions, whereas the locked-winches treatment was the least stable of the three treatments given the changing environmental conditions.

We found both autotrawl systems have a potential to improve bottom trawl survey biomass estimates by increasing the dynamic stability of the trawl, thereby reducing the variance in its catchability. The equal-tension system proved better than the symmetry system in improving the overall stability of the footrope bottom-tending performance given the low bottom current velocities observed. Symmetry autotrawl systems, designed to react to crosscurrent conditions at towing depth, could prove to be more effective under stronger current conditions, but during our experiment, current velocities may have been too low (≤35 cm/s) for us to be able to detect a difference between the symmetry and tension towing modes.

Bridles

Flatfish are stimulated to herd by close proximity to or actual contact with the lower bridle (Main and Sangster, 1981a), whereas semipelagic species such as Atlantic cod (*Gadus morhua*) are probably stimulated to herd by the sight of the otter doors and mud clouds created by the doors and lower bridles (Main and Sangster, 1981b). For this reason, the length of the lower bridle in contact with the bottom and the frequency of this contact affect the herding efficiency of the trawl (Somerton, 2003). If the among- and within-tow variability of the bridle bottom-tending distance could be reduced by using an autotrawl system, then standardizing survey

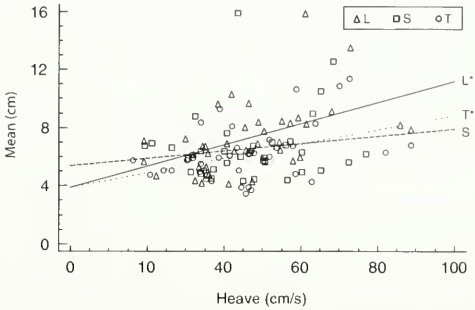

Figure 8

Comparison of regression lines illustrating the relationship between mean bridle distance off-bottom and heave for locked winches (L), symmetry (S), and tension (T) treatments. Treatments in which the heave had a statistically significant effect on the mean are identified with an asterisk (*).

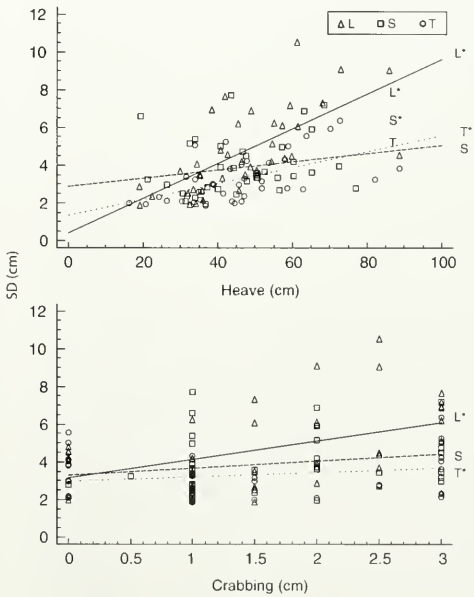

Figure 9

Comparison of regression lines illustrating the relationship between standard deviation (SD) in bridle distance off-bottom and environmental variables for locked winches (L), symmetry (S), and tension (T) treatments. Treatments in which the environmental variable had a statistically significant effect on the SD are identified with an asterisk (*).

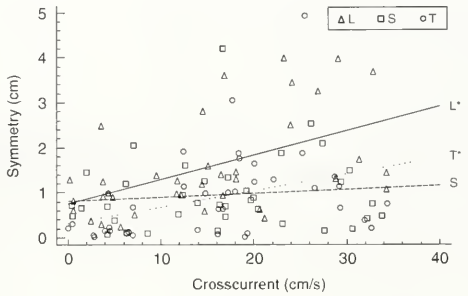

Figure 10

Comparison of regression lines illustrating the relationship between bridle symmetry and crosscurrent for locked winches (L), symmetry (S), and tension (T) treatments. Treatments in which crosscurrent had a statistically significant effect on bridle symmetry are identified with an asterisk (*).

procedures to include towing with an autotrawl system would likely be beneficial.

Our results showed that both autotrawl systems reduced the mean distance of the bridles off-bottom and the standard deviation of this distance and increased the symmetry between bridles (Fig. 4) over the locked-winches treatment. Our experiment also demonstrated that both autotrawl systems increased the stability of lower bridle bottom contact in changing environmental conditions, but we were unable to discern which of the systems was better. The data indicate that bridle bottom-tending performance was the least affected by environmental conditions during the symmetry treatment; however the standard deviation in the bridle distance off-bottom was almost always lower during the tension treatment, the exception being under extreme heave conditions (Fig. 9). The locked-winches treatment had the highest standard deviation and was affected the most by heave, crabbing, and crosscurrent velocity.

Autotrawl systems counteract the effects of warp length differential created by trawl crabbing. During our locked-winches treatment crabbing likely caused unequal tension in the warps similar to that seen while towing straight behind the boat with unequal warp lengths. Weinberg and Somerton (2006) reported that warp tension changes significantly with offset in warp lengths. To compensate for the crabbing angle and to assure that the trawl is pulled square to the direction of the tow during crabbing, one warp should be shorter than the other. Tension-controlled autotrawl systems adjust the length of the warps to equalize the tension on them. Symmetry-controlled autotrawl systems change the length of the warps to minimize crosscurrent and also increase the symmetry of the trawl in relation to the tow direction.

In summary, autotrawl systems proved to be effective in decreasing some of the adverse effects of environmental factors on some aspects of the 83-112 bottom trawl performance and, as a result, have the potential to reduce variance in among-haul catchability of the survey trawl. For this trawl, footrope and bridle distances off-bottom were significantly different among the three towing modes, albeit the differences in actual distances off-bottom were small. Trawls deploying heavier groundgear, thus enabling more constant contact with the bottom, may not be as affected. Further investigations are needed to assess the effects of the two types of autotrawl systems on other types of survey trawl gear, such as high-opening bottom trawls, trawls using different footropes, shrimp trawls, and midwater trawls. The effect of using autotrawls in areas with stronger current and different depths also needs to be investigated for the different types of trawl gear.

For bottom trawl surveys, we are concerned with two potential shortcomings in the symmetry-controlled autotrawl system tested. First, videos of trawling in rough terrain have revealed footrope distortion occurring when the footrope or doors snag on the bottom (Weinberg, unpublished data). Typically, the side opposite the snag is pulled forward while the snagged side remains stationary or is pulled ahead at a slower pace. This uneven pull on the net causes asymmetry in the headrope shape, by skewing it from the general tow direction (Weinberg and Somerton, 2006). Distortion of the headrope introduces error in the current direction and velocity values obtained by the current sensor mounted on the headrope from which warp length is determined, and thus impacts trawl performance. Our second concern involves the overall warp adjustment period required for the trawl to equilibrate to current

direction and velocity based on the current sensor input. Because many surveys standardize to a 15-min tow duration, a proportionally large percentage of tow time may be involved with adjusting warp lengths in pursuit of optimal symmetry and therefore vary trawl catchability during the tow. Under commercial trawling conditions, the manufacturer of the symmetry winch control system recommends using a 2-min minimum signal collection and analysis period between warp adjustments. After each adjustment, new sensor signals would be received and evaluated, followed by another warp adjustment, if necessary. We are uncertain as to how many warp adjustments may be necessary to orient the trawl in relation to crosscurrent flow, but based on our experiences and the frequency with which warp lengths changed during our experiment, it is conceivable that several adjustment periods spanning the majority of the survey tow may be necessary, leaving minimal time for the net to actually fish symmetrically. Furthermore, each 2-min warp adjustment would be based on a maximum of only five current flow readings because the current sensor refreshes data at 24-s intervals. Should signal loss occur, then fewer data points would be available.

We recommend taking a cautious approach before switching a trawl survey from locked winches to autotrawl. A change in survey method may require an extensive calibration experiment between the two trawling methods in order to maintain the continuity of a survey time series. Furthermore, autotrawl systems, like other mechanical devices, require service, appropriate inspections and periodic testing to ensure that they are functioning correctly within manufacturer specifications. Autotrawl calibration parameters are dependent upon accurate measurements of the diameter and length of each winch drum, warp diameter, and construction (e.g., compacted vs. traditional or wire core vs. fiber core), layers of warp, and the number of windings per layer on each drum. Hydraulic pumps and lines, electric motors, valves, solenoids, computerized control panels, and geometric counters must all be inspected to assure proper operation. Of course, should surveys operate with a symmetry-style autotrawl system, then all of the above procedures would hold true in addition to the need for accurate calibration of the current sensor and the proper mounting of the sensor to the headrope.

Acknowledgments

The success of this project is due to the efforts of many. We extend our gratitude to Tim Cosgrove, Brad Lougheed, and the crew of the FV *Vesteraalen*. Our knowledge of winch control systems was greatly enhanced by the guidance of Doug Dixon and Ed Ramberg, as was our ability to communicate at-sea with a wide range of instruments thanks to Scott Furnish, David Roetcisoender, Jon French, and Dennis Benjamin. We are also grateful to our reviewers including Captain John Gruver, Mark Wilkins, Gary Walters, and Peter Munro.

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The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida), from 1981 through 2003

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Abstract—The California market squid (*Loligo opalescens*) has been harvested since the 1860s and it has become the largest fishery in California in terms of tonnage and dollars since 1993. The fishery began in Monterey Bay and then shifted to southern California, where effort has increased steadily since 1983. The California Department of Fish and Game (CDFG) collects information on landings of squid, including tonnage, location, and date of capture. We compared landings data gathered by CDFG with sea surface temperature (SST), upwelling index (UI), the southern oscillation index (SOI), and their respective anomalies. We found that the squid fishery in Monterey Bay expends twice the effort of that in southern California. Squid landings decreased substantially following large El Niño events in 1982–83 and 1997–98, but not following the smaller El Niño events of 1987 and 1992. Spectral analysis revealed autocorrelation at annual and 4.5-year intervals (similar to the time period between El Niño cycles). But this analysis did not reveal any fortnightly or monthly spawning peaks, thus squid spawning did not correlate with tides. A paralarvae density index (PDI) for February correlated well with catch per unit of effort (CPUE) for the following November recruitment of adults to the spawning grounds. This stock–recruitment analysis was significant for 2000–03 ($CPUE=8.42+0.41PDI$, adjusted coefficient of determination, $r^2=0.978$, $P=0.0074$). Surveys of squid paralarvae explained 97.8% of the variance for catches of adult squid nine months later. The regression of CPUE on PDI could be used to manage the fishery. Catch limits for the fishery could be set on the basis of paralarvae abundance surveyed nine months earlier.

Manuscript submitted 7 May 2004
to the Scientific Editor's Office.

Manuscript approved for publication
20 June 2005 by the Scientific Editor.

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The recent discovery of falsification in Chinese fisheries reporting has led to the realization that the majority of the world's fisheries surpassed sustainability in 1988 (Watson and Pauly, 2001). The food chain has been fished down by removal of apex predators like swordfish and snapper beyond sustainability, and fisheries have subsequently shifted to prey items like sardine and mackerel (Pauly et al., 1998). We have reached the point where cephalopods are regularly the largest biomass of all commercial species harvested. Since 1970, groundfish landings of flounders, cods, and haddocks have either decreased or maintained their levels while landings in cephalopod fisheries have increased (Caddy and Rodhouse, 1998). Some of the larger cephalopod landings may be due to increased demand, but lower levels of predation and competition from finfish, and the shorter lifespan of squid may have allowed cephalopods to increase in abundance worldwide.

Loligo opalescens is a small squid (130 mm mantle length) that occupies the middle trophic level in California waters, and it may be the state's most important forage species. Market squid are principal forage items for a minimum of 19 species of fishes, 13 species of birds, and six species of mammals (Morejohn et al., 1978). The effective management of this fishery is of paramount importance not only to the fishermen involved but also to the millions of fishes, birds, and mammals that compete for this resource. Because cephalopods eat mostly zooplankton (Loukashkin, 1976), if we also deplete the squid population, it is not clear how oceanic food chains will respond. If the subannual population of *L. opalescens* fails to recruit a large biomass in a given year, the long-lived predators of this species in

the California Current may encounter severe metabolic stress.

Since the decline of the anchovy fishery, market squid probably constitutes the largest biomass of any single marketable species in the coastal environment of California (Rogers-Bennett, 2000). In the 1999–2000 season, fishermen landed 105,005 metric tons of California market squid (*Loligo opalescens*) with an exvessel (wholesale) revenue of $36 million (California Department of Fish and Game [CDFG] landing receipts). These squid deposit egg capsules on sandy substrates at depths of 15–50 m in Monterey Bay (Zeidberg et al., 2004) and 20–90 m in the Southern California Bight. The majority of squid landings occur around the California Channel Islands, from Pt. Dume to Santa Monica Bay, and in southern Monterey Bay. The fishery comprises chiefly light-boats with high wattage illumination to attract and aggregate spawning squid to the surface, and seine vessels that net the squid (Vojkovich, 1998).

Management to date has followed methods that are not dependent upon an estimate of population abundance because no estimate of squid biomass exists. In addition to limiting the catch and the number of vessels, management of the fishery has included weekend closures north of Point Conception since 1983, and these closures have recently extended to all of California coastal waters. This regulation is designed to allow a 48-hour period each week for undisturbed spawning. For Monterey Bay, the weekend closure resulted in highest landings on Mondays and decreasing daily landings through Friday (Leos, 1998). Since 2000, light boat and seine vessel operators have been required to complete logbooks for CDFG, such that CPUE can be estimated from data on the cumulative effort required to land squid.

Because of their short lifespan, many squid populations have been more effectively correlated with local oceanographic conditions than have pelagic fish species with life spans of 4–8 years. Squid landings from all regions of the world fluctuate in conjunction with the temperatures of the previous season. McInnis and Broenkow (1978) found positive temperature anomalies preceded good *Loligo opalescens* landings by 18 months, and poor squid catches followed periods of anomalous low temperatures in Monterey Bay. Robin and Denis (1999) found similar results. Warmer waters (mild winters) were followed by increased cohort success for *Loligo forbesi* in the English Channel, but this effect was not constant throughout the year. Conversely, Roberts and Sauer (1994) found *Loligo vulgaris reynaudii* landings in South Africa to increase with upwelling that coincided with La Niña (cold water) conditions in the equatorial Pacific. Rocha et al. (1999) also found an increase in squid paralarvae of many species during upwelling conditions on the Galacian-coast.

Modern instruments for monitoring coastal ocean conditions, including weather buoys and satellites, provide a vast amount of information on the physical environment of fish and squid populations. The correlation between cold, upwelled nutrient-rich water at the sea surface resulting from Eckman transport and phytoplankton blooms a few days later is well established (Nezlin and Li, 2003). Mesoscale eddies generated by coastal processes and islands also serve to concentrate phytoplankton (Falkowski et al., 1991; Aristegui et al., 1997; DiGiacomo and Holt, 2001). The subsequent effect upon zooplankton grazers rapidly follows the cycles of upwelling and relaxation (Wing et al., 1995; Graham and Largier, 1997; Hernandez-Trujillo, 1999).

Waluda et al. (1999) found that the CPUE for the *Illex argentinus* fishery was not related to monthly local sea surface temperature (SST), but CPUE was inversely related to SST on the hatching grounds for the previous July, when hatchlings were in their exponential growth phase (Yang et al., 1986; Grist and des Clers, 1998). The largest catches followed cold water. Waluda et al. (2001) found a large CPUE when the Brazilian Current dominated and frontal waters diminished in the location where squid hatching occurs. Agnew et al. (2000, 2002) found that CPUE for *Loligo gahi* was inversely correlated with SST for hatching areas six months earlier. Sakurai et al. (2000) found that *Todarodes pacificus* CPUE was highest following periods when there were large regions of hatchling-favorable habitat (17–23°C waters). They found a positive correlation between the density of paralarvae and the catch per unit of effort (CPUE) of adults in the same year (r^2=0.91) and also in the CPUE of the following year (r^2=0.77).

The CDFG has an extensive database of landings data from 1981 to the present for market squid. Because there is no record of effort prior to 2000 and because the market is driven by demand, it is difficult to use landings and vessel-day data to calculate a CPUE and therefore estimate biomass. Fishermen report that even if squid are available, they may not be harvested when processors are not accepting squid (Brockman[1]). However, there is no other database as large and widespread temporally and spatially as fishery data. Even though there are no data recorded when boats attempt to catch squid and fail, we can still use landings and vessel-days to create a CPUE. This CPUE therefore is not a methodically collected estimate of biomass, but is still a robust enough estimate of abundance to draw preliminary conclusions as we wait for logbook data to accumulate.

It is important to determine the effects of the environment on the California market squid fishery so that we can predict future landings from present conditions. Our investigation uses California market squid landings for 1981–2003 to examine correlations of landings and CPUE with physical oceanography. We compare landings data (time, location, vessel-days, and landings [in pounds]) to sea surface temperature (SST), upwelling index (UI), the Southern Oscillation index (SOI), the index of sea surface temperature in the eastern equatorial tropcial Pacific NINO3, and their respective anomalies. We also compare CPUE to a paralarvae density index

[1] Brockman, D. 2002. Personal commun. Davies Locker Sportfishing, 400 Main St. Newport Beach, CA 92611.

(PDI) based upon distributions determined in the Southern California Bight (Zeidberg and Hamner, 2002).

Materials and methods

The CDFG database for commercial California market squid landings from 1981 to present includes weight, date, location (based on CDFG 10×10 nm blocks), and gear type. Accounting for general physical oceanographic properties (Harms and Winant, 1998; Bray et al., 1999; Brink et al., 2000; Hickey et al., 2003) and following our previous studies (Nezlin et al., 2005), we organized the landings data into six areas to look at subtle differences between them: MB=northern coastal (because the majority of the landings in this area occur in southern Monterey Bay), CC=central coastal, SB=Santa Barbara Channel, SCB=Southern California Bight, SM=Santa Monica, and SD=San Diego. Also we grouped the fishery into two larger regions April (APR, equal to MB above) and October (OCT, a combination of the other five areas) based upon the month of greatest recruitment (Fig. 1). For the purpose of our study, recruitment is the aggregation of reproductive adults on the spawning grounds. When CDFG reports squid data, they make a distinction at Point Conception, thus our MB and CC areas are grouped as the "north" and our SB, SCB, SM, and SD are named "south." For this fishery we defined CPUE as the recorded tons landed in a day, divided by the number of seine vessels that landed these squid. Those days in which there were no landings were assigned a value of zero. This CPUE is important because, although not truly a quantifying effort, it does provide a means for estimating the abundance of squid by providing some basis for the amount of time taken to make a landing. Lampara, brail, and light boat data were not included because of increased variability in landings and effort and the fact that these vessels have dwindled from ten to zero percent since 1981.

The landings and boat data for each area were summed for each block by day. For example, assume that on a particular day fishermen caught 10,000 metric tons with four boats in the area of SM, 18,000 tons from three boats in SCB, and 12,000 tons from three boats in SB. We would calculate a CPUE of 2500 tons/vessel-day in SM, 6000 tons/VD in SCB, and 4000 tons/VD in SB, respectively. Thus for every date for which there was a landing we were able to calculate CPUE value for each area. Until 2002, there had never been a landing in Monterey in January, when one vessel captured 75 tons. Data such as this produce misleadingly high CPUEs; therefore all months with less than seven vessel-days for the entire 22-year period were removed from the analysis.

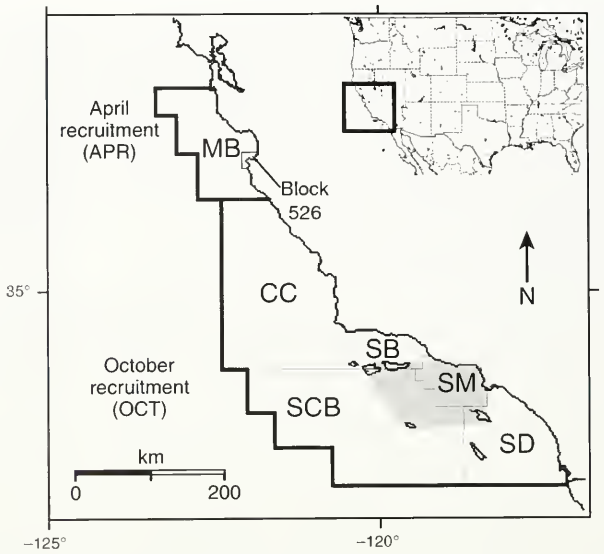

Figure 1

The California coast with the fishery areas for the California market squid (*Loligo opalescens*) identified. Areas were classified according to physical oceanographic features: Northern Coast (MB), Central Coast (CC), Santa Barbara Channel (SB), Southern California Bight (SCB), Santa Monica Bay (SM), and San Diego (SD). Regions were also classified by fishery recruitment month: April recruiting (APR: same as MB area) and October recruiting (OCT: CC, SB, SCB, SM, and SD areas combined). Block 526 (indicated with a slender arrow) is where the majority of the MB-APR landings occur. Shaded area indicates the location of the paired-net surveys used to generate the paralarvae density index (PDI).

Physical oceanography data were gathered from the Internet for sea surface temperature (SST),[2] upwelling index (UI),[3] southern oscillation index (SOI),[4] and NINO3.[5] Upwelling index (UI) is an Ekman offshore water transport (m^3/s per 100 m of the coastline) estimated from fields of atmospheric pressure (Bakun, 1973). Southern Oscillation index (SOI) is the difference between the standardized measurements of the sea level atmospheric

[2] NOAA (National Oceanic and Atmospheric Administration). National Data Buoy Center. 2000. Website: http://facs.scripps.edu/surf/buoys.html [Accessed on 24 April 2003.]

[3] NOAA Pacific Fisheries Environmental Laboratory. 2003. Website: http://www.pfeg.noaa.gov/products/las.html [Accessed on 20 March 2003.]

[4] Australian Government Bureau of Meteorology. 2005. Website: http://www.bom.gov.au/climate/current/soihtm1.shtml [Accessed on 29 March 2003.]

[5] IRI (International Research Institute for Climate Prediction). 2005. Website: http://ingrid.ldgo.columbia.edu/SOURCES/.Indices/.nino/.EXTENDED/.NINO3/ [Accessed on 20 April 2004.]

Table 1

Totals of vessel-days, landings (metric tons), and CPUE (tons/vessel-day) for two time periods of the California market squid (*Loligo opalescens*) fishery (1981–2003). The majority of the fishery occurred in Monterey Bay, 1981–89, and in southern California, 1990–2003. The six small areas represent physical oceanographic features and the larger regions (APR and OCT) are grouped by the month of greatest recruitment of spawning adults to the fishery (see bolder border in Fig. 1). MB and APR are synonymous terms. MB=northern coastal area, predominantly southern Monterey Bay; CC=central coast; SB=Santa Barbara; SCB=Southern California Bight; SM=Santa Monica; and SD=San Diego. VD=vessel days.

Years	Region and area	Vessel-days (VD)	Percent VD	Landing (tons)	Percent landings (tons)	CPUE (tons/VD)
1981–89	APR					
	MB	4918	87.4	27242	66.5	5.5
	OCT					
	CC	38	0.7	1040	2.5	27.4
	SB	186	3.3	3811	9.3	20.5
	SCB	169	3.0	3475	8.5	20.6
	SM	122	2.2	1811	4.4	14.8
	SD	194	3.4	3597	8.8	18.5
Subtotal		709	12.6	13735	33.5	19.4
Total		5627		40977		7.3
1990–2003	APR					
	MB	6508	22.5	92323	13.6	14.2
	OCT					
	CC	1283	4.4	33964	5.0	26.5
	SB	3822	13.2	104172	15.3	27.3
	SCB	8037	27.7	212986	31.3	26.5
	SM	4408	15.2	113569	16.7	25.8
	SD	4918	17.0	124147	18.2	25.2
Subtotal		22468	77.5	588838	86.4	26.2
Total		28976		681161		23.5

pressure in Tahiti and Darwin. NINO3 is determined by averaging the SST anomalies over the eastern tropical Pacific (5°S–5°N; 150°W–90°W). The buoys used were the Monterey buoy (46042, 36°N 122°W) for the MB region, the east Santa Barbara buoy (46053, 34.24°N 119.85°W) for the SB region, and the Santa Monica buoy (46025, 33°N 119°W) for the remaining regions.

We performed a spectral analysis of the entire time series to look for significant periodicities in the daily data for the entire 22-year data set. CPUE values were natural log-transformed and smoothed with a Parzen window (Ravier and Fromentin, 2001). We used a time series analysis method of cross correlation to determine the lag period in months between CPUE and the physical features of SST, SOI, NINO3, and UI and their anomalies from averaged seasonal cycles. Using this lag period we calculated linear regression of the CPUE from SST.

Sea surface temperature (SST) time series was obtained from infrared satellite measurements with advanced very high resolution radiometers (AVHRRs) on National Oceanic and Atmospheric Administration (NOAA) meteorological satellites. The data were processed at the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS) and the NOAA National Oceanographic Data Center (NODC) within the scope of Pathfinder Project (version 4.1, available from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center [JPL PO DAAC]).[6]

We performed a stock-recruitment analysis from a paralarvae density index (PDI). Paralarvae were collected with paired nets (505-μm mesh) without bridles, deployed like bongo-nets, and towed in a double oblique mode to 100 m depth. Samples were taken in February from 1999 to 2003, every 7.5 km on transects in regions SCB and SM (Zeidberg and Hamner, 2002). Flow meters were used to standardize the number of paralarvae per 1000 m^3 of water. The PDI is the average number of paralarvae/1000 m^3 from all tows. We used linear regression to compare the February PDI with the CPUE for the large November adult recruitment event in the SCB and SM regions of the same year.

Statistics were performed with Statview 3.0 (Abacus Concepts, Berkeley, CA) or Statistica 6.0 (Statsoft, Tulsa, OK). Interpretations of *t*-test, regression, ANOVA,

[6] http://podaac.jpl.nasa.gov/ [Accessed on 15 March 2003.]

spectral analysis, and cross correlation time series were made in accordance with Zar (1984).

Results

Decadal-regional analysis

The 22-year fishery data for *Loligo opalescens* were divided into two periods: 1981–89 and 1990–2003 (Table 1) due to a southward shift in the fishery after 1989. For the first period (1981–89), 87% of the effort and 66% of the landings were predominantly focused in the MB or APR region, specifically in the southern portion of Monterey Bay. The amount of squid captured in 1981 and 1982 was not matched again in Monterey Bay until 2002. The MB region was the most focused region; 62% of the total catch and 83% of the CPUE came from a very small area (block 526, Fig. 1)—just off Monterey harbor. CPUE in this region and time period was low, 5.54 tons/vessel-day (Table 1). SM had 4.43% of the landings and 2.2% of the vessels, yielding a CPUE of 14.85 tons/vessel-day. The SB, SCB, and SD areas were similar in the 1980s with landings around 9%, vessels at 3%, and CPUEs varying from 18.5 to 20.5 tons/vessel-days. The CC area had the smallest percentage of landings (2.5%) and vessels (0.7%), but the highest CPUE (27.4%)—most likely due to squid being hauled as a secondary target species in this region. Few fishermen choose to harvest squid in the central California area because of rough seas and rocky, gear-fouling ocean bottoms.

The focus of the market squid fishery shifted to southern California in the 1980s and landings surpassed those of Monterey Bay in 1990 (Fig. 2, Table 1). Whereas vessel-days per year decreased by 17.6% in the MB area, vessel-days increased 20-fold in the other areas. For the period 1990–2003, SM and SB ranked third and fourth for landings and vessel-days because of hauls made on the northern coasts of the Channel Islands and off the Malibu and Redondo Canyons, respectively. CC is the area least targeted, with only 5% of landings and vessels. CPUE for this period was 26 tons/vessel for all areas except MB, where it was little more than half that at 14 tons/vessel. CPUE in APR/MB has nearly tripled since 1981–82. CPUE in the OCT region has increased more modestly, except in SM.

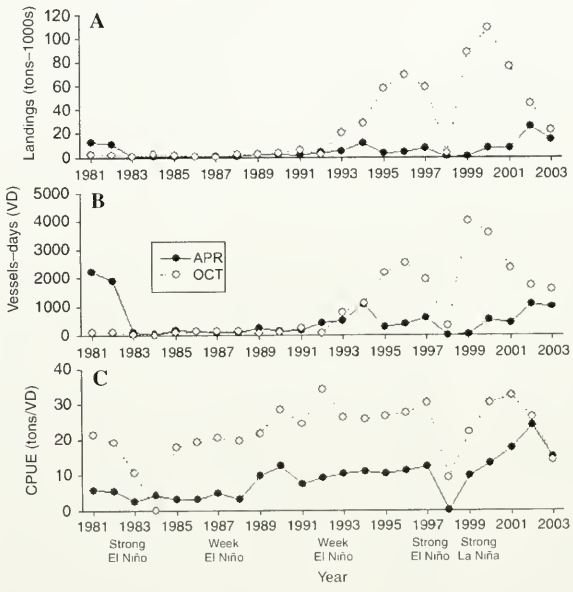

Figure 2

Fishery data for *Loligo opalescens*, summed by year for 1981–2003. (**A**) landings, (**B**) vessel days, and (**C**) catch per unit of effort (CPUE) by year for Monterey Bay (April [APR]—black circles) and southern California (October [OCT]—unfilled circles) regions. Scale of *y*-axis changes between A, B, and C. Note the lack of landings in OCT in 1984 and APR in 1998, following strong El Niño events.

Since 1999, annual landings have decreased in OCT (91,229 tons to 22,180 tons) and increased in APR (289 to 14,521 tons—with 22,770 tons in 2002, Fig. 2A). Effort has increased as well in the last 23 years (Fig. 2B). With the exception of MB 1981–82, all areas saw the number of vessel-days/month increase until the 1997–98 season. The number of vessel-days has decreased since 1999—in OCT (4011 to 1573)— and has increased in APR (20 to 978). The average number of days between landings for individual boats in APR (2.3) and OCT (2.1) was not significantly different (t-test$_{0.05(2)}$, df=977, t-value 0.87, P=0.39).

There have been increases in CPUE concomitant with gains in experience, and advances in technology have enhanced the ability of fishermen to locate squid. There has been a "ratcheting up," both in terms of size of vessel and in the amount of sonar (from single to dual frequency [50 to 200 kHz]) used in the competition among fishermen. However, CPUE decreased substantially in all regions in 1984 and 1998, the second years of the two biggest El Niño events recorded. Milder El Niño events in 1987 and 1992 preceded dips in CPUE values in 1988 and 1993 (Fig. 2C). Average CPUE was calculated for the APR and OCT regions by splitting the data

by the frequencies determined from the spectral analysis. These splits resulted in three separate means for CPUE in APR (7.5-year frequency) and five means for the OCT region (4.5-year frequencies). Anomalies of CPUE from these means were compared to the climatic indices, and had significant linear regressions to NINO3, SOI, and UI anomalies, but explained less than 5% of the variance (data not shown).

1981–2003 squid fishery data

In comparisons of landings (Fig. 3A) by month, the six areas fell into two categories: APR and OCT. Effort in vessel-days and CPUE showed similar trends. The *Loligo opalescens* squid fishery generally occurs from April through November in APR. Although landings peak in May, by then there are so many vessels in operation that CPUE has dwindled to half that of April (Fig. 3, B and C). There is a second landings pulse in August.

In the five areas of the OCT grouping, landings typically begin in October, build to a peak in January, and diminish to lows in August (Fig. 3A). A large unimodal pulse of squid landings occurred in November for all areas except SCB. The SCB had a bimodal recruitment pulse, the two largest recruitment events in all of California: one in November and a larger one in January. In SD, like SCB, landings peaked in January, but there was no strong November signal in this region.

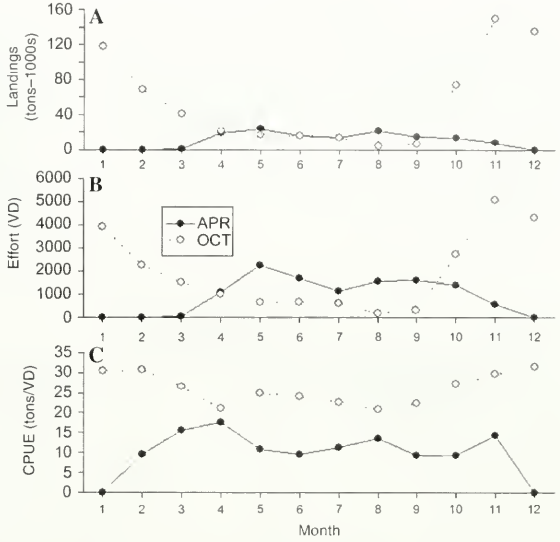

Figure 3

Fishery data for *Loligo opalescens*, summed by month for 1981–2003. (**A**) Landings (metric tons). (**B**) Effort in vessel-days (VD). (**C**) Catch per unit of effort (tons/VD). Monterey Bay (April [APR]—black circles) and southern California (October [OCT]—unfilled circles). Scale of y-axis changes between A, B, and C. Largest landings occurred one month later in May in the APR region and in November in the OCT region when SST was 11.7°C and 16.1°C, respectively.

CPUE by month for APR was typically half that of OCT. The APR CPUE varied between 8 and 20 tons/vessel-day, for months with more than seven vessel-days, whereas CPUE for the southern California (OCT) areas ranged from 17–36 tons/vessel-day (Fig. 3C).

Time-series analysis

The periods of the ten highest peaks of the variance spectrum were determined for all six areas (Table 2). The largest peaks from the spectral analysis occurred at periods of 372 and 356 days, or roughly 1 year for all areas. There was a 7.5-year peak in the MB and CC areas. There was a 4.5-year peak (for all areas except MB) that was similar to the period of the four El Niño events that occurred in this area during the 22-year period. There was a 3.7-year peak for all areas except CC and SM. The seven-day cycle is most likely a stochastic factor of fishermen working within weekend closures because data before 1998 did not have this periodicity. There was no 28- or 14-day cycle in any of the areas; this finding likely indicates that spawning squid do not respond to tidal currents or lunar light.

The most significant cross correlations of time lag analysis for CPUE to SST are listed in Table 3. In all cases of biological significance, CPUE lagged SST by 4, 5, or 10 months. MB CPUEs were highest (in May) when SST was low four months earlier (Jan), and hence gave a negative correlation. In all other regions, the four or five month correlation was positive, with CPUE high (Nov) when SSTs were high four months earlier (Jul). For the southern California areas there was a negative correlation with SSTs 10 months earlier (Jan). Therefore, cold winters and warm summers correlate with larger landings. Recruitment of spawning adults to the fishery occurs during the productive seasons in both APR, MB, and OCT. Productivity in APR and MB co-occurs with the spring–summer upwelling season, and in OCT productivity correlates with winter storms that lead to a deeper mixed layer. There were significant cross correlations with SOI, NINO3, and UI, but not with the anomalies of SOI and UI. Interestingly correlations for NINO3 were greater than those for SOI (Fig. 4), indicating that the CPUE of *Loligo opalescens* is more closely related to the "oceanic teleconnection" than to "atmospheric teleconnection."

Table 2

Periods of greatest spectral variance in the daily CPUE data of the market squid (*Loligo opalescens*) fishery for 1981–2003. Significance: $P<0.01$. Numbers in bold are repeated in more than one area. Harmonics of factors of 2: 2, 4, ... 4096 (blank spaces) are omitted because they are inherent in spectral analysis and not relevant to this species. MB=northern coastal area, predominantly southern Monterey Bay; CC=central coast; SB=Santa Barbara; SCB=Southern California Bight; SM=Santa Monica; and SD=San Diego.

	Top ten periods of spectral variance					
	MB			CC		
Rank	Days	Years	Month	Days	Years	Month
1	**372.4**	1	12.2			
2	**356.2**	1	11.7	**372.4**	1	12.2
3				**1638.4**	4.5	53.7
4	**7**	0	0.2	**2730.7**	7.5	89.5
5	**315.1**	0.9	10.3	**455.1**	1.2	14.9
6	**2730.7**	7.5	89.5	481.9	1.3	15.8
7	**341.3**	0.9	11.2	**356.2**	1	11.7
8	**455.1**	1.2	14.9	**390.1**	1.1	12.8
9	3.5	0	0.1			
10	**1365.3**	3.7	44.8			
	SB			SCB		
Rank	Days	Years	Month	Days	Years	Month
1	**372.4**	1	12.2	**372.4**	1	12.2
2	**356.2**	1	11.7	**1638.4**	4.5	53.7
3	**390.1**	1.1	12.8	**356.2**	1	11.7
4	**1365.3**	3.7	44.8	**1365.3**	3.7	44.8
5	**1638.4**	4.5	53.7	**390.1**	1.1	12.8
6	910.2	2.5	29.8			
7						
8	264.3	0.7	8.7			
9				819.2	2.2	26.9
10	**182**	0.5	6	**682.7**	1.9	22.4
	SM			SD		
Rank	Days	Years	Month	Days	Years	Month
1	**372.4**	1	12.2	**356.2**	1	11.7
2	**1638.4**	4.5	53.7			
3	**182**	0.5	6	**372.4**	1	12.2
4				**182**	0.5	6
5				**1638.4**	4.5	53.7
6	**356.2**	1	11.7	**682.7**	1.9	22.4
7	**390.1**	1.1	12.8	**341.3**	0.9	11.2
8	**315.1**	0.9	10.3	**1365.3**	3.7	44.8
9	204.8	0.6	6.7	**390.1**	1.1	12.8
10	**7**	0	0.2	178.1	0.5	5.8

Table 3

Results of the time series analysis. Significant correlation coefficients occurred when CPUE lagged behind sea surface temperature (SST) from buoys and advanced very high resolution radiometers (AVHRRs) by 4–10 months for all areas, except CC. Negative correlation coefficients demonstrate that high CPUE corresponds with low water temperatures in the lagged month from column two; positive values may indicate a direct relationship. MB=northern coastal area, predominantly southern Monterey Bay; CC=central coast; SB=Santa Barbara; SCB=Southern California Bight; SM=Santa Monica; and SD=San Diego.

CPUE region	Lagged (months)	SST source	Correlation coefficient
MB	4	MB buoy	−0.481
	5	AVHRR	−0.358
SCB	4	SM buoy	0.206
	10	SM buoy	−0.344
	9	AVHRR	−0.340
SD	4	SM buoy	0.220
	10	SM buoy	−0.398
	10	AVHRR	-0.387
SM	5	SM buoy	0.176
	10	SM buoy	−0.340
	10	AVHRR	−0.334
SB	4	ESB buoy	0.387
	4	SM buoy	0.415
	9	AVHRR	−0.372

Assuming a 6–9 month lifespan for *L. opalescens*, we used linear regression to compare SST from buoy data for the previous 6–10 months. We performed comparisons up to 10 months because squid eggs take 30 days to hatch at 12°C, which is a typical time period for eggs to hatch in winter in Southern California and spring–summer in Monterey Bay. The only significant regression occurred in the SM region with SSTs 10-months earlier ($r^2=0.46$, $P=0.0033$, Fig. 5). We compared satellite-derived (AVHRR) estimates of SST for 1985–2002 from areas with high densities of paralarvae and juveniles (within 8 km of shore) with CPUE by using cross correlation time series analysis. Although there were significant correlations, linear regression yielded no significant predictions for landings or CPUE from SST.

Stock recruitment analysis

We compared a paralarvae density index (PDI) with CPUE for the SCB and SM regions (Fig. 6, shaded area of Fig. 1). Collections of paralarvae were made in February (Fig. 6). After the initial surveys of 1999, methods developed in Zeidberg and Hamner (2002) resulted in 34–50 stations for oblique bongo tows to collect paralarvae in SCB and SM regions. Paralarvae/1000 m^3 from

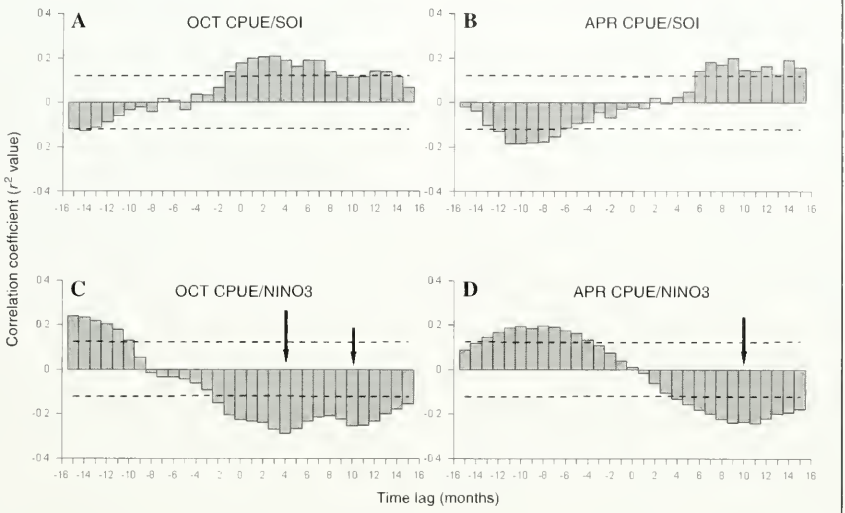

Figure 4

Time-series analysis: cross-correlation between CPUE and the global climatic indices: Southern Oscillation index (SOI for atmospheric pressure differences between Tahiti and Darwin, **A** and **B**) and NINO3 (SST anomaly in eastern equatorial Pacific, **C** and **D**) for regions OCT (A, C) and APR/MB (B, D). The correlation between CPUE and NINO3 is greater than the correlation between CPUE and SOI in both regions. CPUE lags NINO3 by 9–11 months in APR and 4 months in OCT. Thus, the effects of an El Niño event cause declines in CPUE for *Loligo opalescens* in Southern California 4 months later and in Monterey Bay 9–11 months later (long arrows). High correlation coefficients at a 10-month lag in Southern California (OCT) may be due to a second generation of market squid responding to changes in SST (shorter arrow).

all stations were averaged to create the February PDI (Fig. 6 lower right), and this PDI was then compared to the November recruitment of spawning adults (CPUE) to the fishery for the same year. Linear regression was not significant for 1999–2003 (r^2=0.522, P=0.1683). However, if 1999 was treated as an outlier because it lacked nearshore sampling sites where 76% of the paralarvae were captured subsequently, the regression explains 97.8% of the variance, and the F-value of the ANOVA ratio test for this regression is significant, P=0.007 (Fig. 7). From 1992 through 2002, SCB (36.2%) and SM (16.2%) represented nearly half of the landings for the state, and therefore this technique (regression of CPUE on PDI) could apply throughout the state.

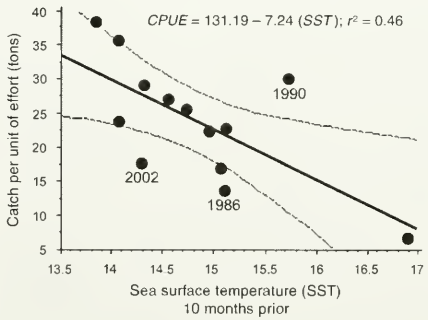

Figure 5

Linear regression and 95% confidence intervals for CPUE in November, the highest recruitment month, from SST of the previous January in the SM region. $CPUE$=131.19 – 7.24×SST; r^2=0.46, P=0.0033.

Discussion

We report landings, effort, and catch per unit of effort for *Loligo opalescens* in California for 1981–2003. It is important to reiterate that CPUE is an approximation of abundance in the fishery and fails to estimate biomass of squid in California waters. Vessels that attempt to cap-

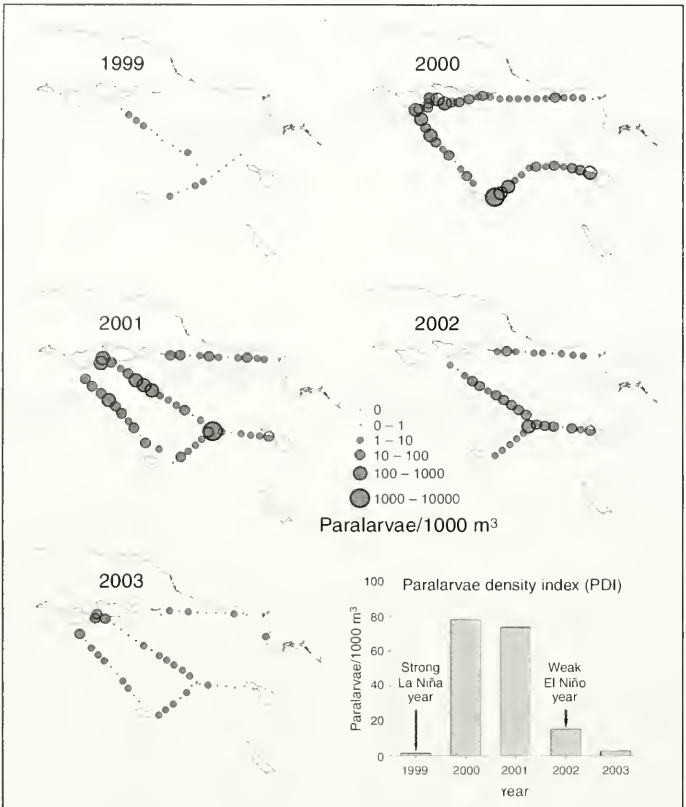

Figure 6

Density profiles (exponential bubble plot) for *Loligo opalescens* paralarvae in the Southern California Bight, February 1999–2003 (shaded area of Fig. 1). Size of circles corresponds to number of paralarvae/1000 m^3 seawater sampled. Data for 1999–2001 reprinted with permission from Springer-Verlag, originally in Zeidberg and Hamner (2002) Mar. Biol. 141(1):111–122. Data from all tows were averaged to obtain a paralarvae density index (PDI) for each year, lower right. 1999 La Niña (cold) and 2002 El Niño (warm) events are labeled above bars in the index. Note the lack of any sample sites within 8 km of shore or with >100 paralarvae/1000 m^3 in 1999.

ture squid and fail cannot be tracked with this method, and squid that are not harvested commercially are not accounted for in this report. *Loligo opalescens* reproduces by aggregating from small, foraging groups of hundreds of individuals to groups of millions of individuals. It is possible, therefore, that a large decrease in biomass can be masked by a larger percentage of the population aggregating in seemingly similar-size spawning masses. Such species are vulnerable to highly mobile fisheries (Oostenbrugge et al., 2002).

Trends in the fishery

The fishery for market squid (*Loligo opalescens*) has increased in all parts of the study area since 1983 because of an increase in demand for calamari internationally and because of the collapse of other fisheries both within and outside California waters. The majority of fishing activity has shifted from Monterey Bay to the Southern California Bight since the 1980s. Fishing activity in the bight experienced a second increase in

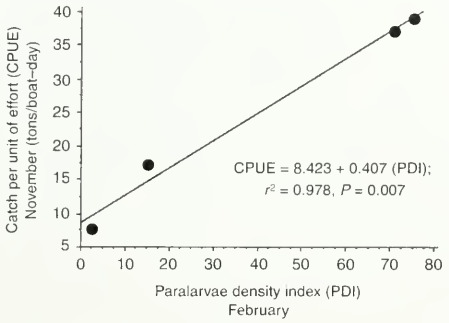

Figure 7

Stock-recruitment model: linear regression of catch per unit of effort (CPUE) for spawning adults in November on the February paralarvae density index (PDI) in the SM and SCB areas for 2000–2003.

the 1990s, reflecting fishery participants from Alaska, Washington, and Oregon. The most economically harmful trend has been the substantial decrease in landings during the second year of strong El Niño events, and the slight decrease in landings after weak ones.

The initial impetus of performing the spectral analysis was to determine if the squid were migrating to the spawning grounds in relation to a lunar or tidal signal. It is important to note that the spectral analysis with CPUE and landings data (not shown) did not show that squid recruit to spawning sites in a fortnightly cycle. There was no 14-day period in any area. Spectral analysis demonstrated periodicities for CPUE of *Loligo opalescens* on scales ranging from days to years. The most common periods for all areas were annual. Varying from 315 to 390 days, annual cycles made up more than half of the top ten signals in the analysis. The 4.5-year cycle corresponds well with the El Niño events of 1982–83, 1987, 1992, and 1997–98 (Hayward et al., 1999). In each of these cases the CPUE anomalies were negative (Zeidberg, 2003). The longest period was 7.5 years in the MB and CC areas. There were evident leaps in the mean CPUE based on mean CPUE ±5 months in MB at mid-1988 and the end of 1995, when out-of-state fishermen began to harvest squid in California (Zeidberg, 2003). Although these leaps may correspond to changes in the biomass of the squid, they are more likely due to enhancements in the capacity of the fishery to capture squid as acoustic and communication technology has improved. The 3.7-year period is probably a statistical harmonic of the 7.5-year period.

Paralarvae density index (PDI) can predict CPUE

Zeidberg and Hamner (2002) have sampled the SCB and SM areas for *Loligo opalescens* paralarvae since 1999 and we used that data to create a paralarvae density index (PDI). CPUE appears to be a better indicator of stock abundance than landings data for squid (Sakurai et al., 2000). Adults recruiting to the fishery in November, measured in CPUE, can be predicted by linear regression from the PDI of February. A regression of the CPUE data from the PDI data for 1999–2003 is not significant, but if 1999 is treated as an outlier the remaining four points (2000–03) create a regression that explains 97.8% of the variance. Our 1999 sampling of paralarvae may not be representative of the fishery because it was the first sampling year and the sampling sites were located farther offshore than those sampled in 2000–03. In 1999 there were no sites within 7.4 km of shore, where 76% of the paralarvae were captured in the following four years of sampling. Despite these caveats, this method could provide the first opportunity to manage California's market squid fishery according to scientifically gathered biological indicators and with very few of the inherent assumptions needed for many other types of forecasting (Mangel et al., 2002). As the years of logbook data accumulate, estimates of CPUE will be more closely related to the actual biomass of the species. By the end of February, we can have a prediction for the CPUE for the following year's adult recruitment. Paralarvae may be the best stage of the life cycle for a fishery prediction because juveniles can escape trawls, fewer assumptions need to be made than with estimates from spawning females (Macewicz et al., 2004), and there is sufficient time (6–9 months) to develop predictions. These predictions could help managers set catch limits and aid fishermen in deciding how to invest in gear for the following season.

In addition to our paralarvae sampling, CalCOFI has sampled the waters of California for zooplankton in a manner similar to ours since 1949. Paralarval distributions for *Loligo opalescens* have been described from these data (Okutani and McGowan, 1969). The greatest difference between the two sampling efforts is the number of stations that are in close proximity to land. The majority of the paralarvae (76%) captured by Zeidberg and Hamner (2002) were at stations less than 8 km from shore, but there is only one CalCOFI station at this proximity to land. After reviewing their surveys and models of larval dispersal (Franks, 1992; Botsford et al., 2001; Siegel, 2003), we predict that a PDI calculated from CalCOFI samples will be substantially lower than ours, but given the long time period of the CalCOFI sampling program, any significant correlations could be more powerful statistically than ours. Furthermore, fishermen could be employed to perform bongo tows for paralarvae in proximity to shore to complement CalCOFI data. If the CalCOFI bongo net data were sorted for *Loligo opalescens* paralarvae, and fishermen collected paralarvae nearshore, Monterey Bay and southern California CPUE could be predicted months in advance. Separate management of the two regions would be necessary given the time lag of recruitment (APR and OCT).

Comparison of fishery data with physical data

We found a correlation between CPUE of the largest recruitment month with SST buoy data from 10 months earlier in the SM area only. There may be physical features specific to this area that increase the correlation between spawning recruitment and SST. For example, SM is a small area, it is close to the buoy, most of the area is sandy bottom, and it contains the Redondo Canyon. Thus if further attempts to match physical oceanography to the biology of a pelagic species were to occur, the Santa Monica Bay could be the most ideal location. But this correlation between CPUE of the largest recruitment month with SST in the SM area may be a seasonal effect because the regression is significant for SST only and not an SST anomaly. Furthermore, we caution that the significance of the correlation between CPUE and SST in SM may be a type-I error because it was the only significant test of the 30 tests run with an alpha level of 0.05. The size of the recruitment event was not strongly related to small deviations from average monthly SST; thus the timing of squid recruitment to spawning grounds in APR and OCT may be tied to annual fluctuations of prey availability and correlations with temperature may be coincidental. The 10-month lag corresponds to the egg-laying date of 9-month-old squid. The lack of a greater number of correlations may be due to the small spatial resolution of the buoy data and the enormous variability of SST data due to mesoscale oceanographic features in the large fishery areas. In some areas the nearest buoy was quite distant from the fishery zone.

To address the spatial distance of spawning grounds from buoys, we compared SSTs derived from satellite AVHRR images with CPUE. AVHRR data were collected from just the shelves and slopes of the six fishery areas because these are the most important areas for the growth of hatchlings and juveniles. Cross-correlation time series analyses were significant at 5–10 month lags (Table 3), but this significance did not translate into any predictive capabilities with linear regression.

Similarly, cross-correlations of CPUE with SOI and NINO3 were significant at a 10-month lag in Monterey Bay and a 4-month lag in the Southern California Bight. Thus the Monterey fishery (10% of landings) is offset by six months (roughly one short cohort) from the SCB fishery. The correlation coefficients for NINO3 were greater than those of SOI, corroborating the idea that the direct influence of the coastal waves ("oceanic teleconnection") is the main source of the changes in the hydrographic and ecological features of the California Current system (Huyer and Smith, 1985; Rienecker and Mooers, 1986; Lynn et al., 1995; Chavez, 1996; Ramp et al., 1997) rather than the ENSO (El Niño Southern Oscillation)-related changes of atmospheric circulation ("atmospheric teleconnection") (Simpson, 1983; Simpson, 1984a, 1984b; Mysak, 1986; Breaker and Lewis, 1988; Breaker et al., 2001; Schwing et al., 2002).

Loliginid life cycles and future management of squid fisheries

The correlation between SST and CPUE in the following season may have resulted from the unique development pattern of teuthids. The use of CPUE as an index of abundance of the population (Sakurai et al., 2000), in combination with studies of squid growth in relation to SST (Jackson and Domeier, 2003), could explain large fluctuations in landings data from year to year. In terms of bottom-up forcing, individual squid health and the resulting population size result from a combination of prey availability and metabolic rates. Squids grow exponentially in the first two months of life and then logarithmically until senescence. In rearing tanks and given a constant food supply, loliginids also grow faster in warmer temperatures (Yang et al., 1986; Forsythe et al., 2001) as their metabolic rates increase (O'Dor, 1982). Grist and des Clers (1998) predicted that annual fluctuations in SST that cause differential growth in squids can lead to younger cohorts hatched in warm temperatures and surpassing in size older cohorts born in colder seasons. Thus in October, a large 6-month-old squid that hatched in April and developed in warm water may spawn with a smaller 9-month-old squid that hatched in the cold waters of January.

However, in the California system and possibly in other upwelling systems the situation is more complex than in rearing tanks. For example, Jackson and Domeier (2003) demonstrated that due to the influences of El Niño and La Niña cycles and upwelling, the mean mantle length of *Loligo opalescens* is shortest when larvae are hatched in the warmest temperatures and longest when hatched in cold waters. Mantle length is also positively correlated with the upwelling index. In the ocean, squid do not have a constant food supply. The high productivity and cold temperatures caused by upwelling and La Niña combined to create a period of rich food resources and lower metabolic rates for squid, probably enhancing the recovery of the fishery in 1999. During the El Niño event the squids were small and less abundant because they had a high metabolic rate due to increased temperatures and were exposed to lower levels of available prey due to decreased ocean productivity. Seasonal maxima of phytoplankton in Monterey Bay occur in summer; but in the southern part of the Southern California Bight productivity peaks in winter (Nezlin et al., 2002). These differences may be an indicator of why the fishery operates in Monterey Bay from April to November, coinciding with the upwelling season, and in the Southern California Bight from November to May, coinciding with less stratification of the water column and more mixing due to winter storms and colder air temperatures.

Lowry and Carretta (1999) corroborated the temperature-induced plasticity of mantle length (ML) from beaks of squid in California sea lion (*Zalophus californianus*) scats and spewings. MLs of squid prey were half the size during El Niño years on San Clemente and Santa Barbara islands. However, at San Nicholas Island during El Niño events, there were both small- and regular-

size squid prey; this finding may indicate that the squid stock moved offshore to find productive waters. Alternatively, San Nicholas sea lions may have been feeding on squids from Baja California. Zeidberg and Hamner (2002) suggested the possibility of a northern shift of the squid population in El Niño years, as has been found for most zooplankton (Colebrook, 1977).

However, the growth plasticity and fluctuating reproductive success for *Loligo opalescens* should not be underestimated. The possibility remains that the huge fluctuations in squid landings during strong ENSO events is due to the entire biomass of market squid waning and waxing rather than to population migrations away from traditionally fished spawning grounds. Triennial groundfish surveys demonstrate that market squid experienced a coast-wide population decrease, not a poleward migration during the 1997–98 El Niño.[6]

With the exception of El Niño years, the fishery increased its landings each year until 2000. However, it remains unknown if the capacity of the fishery is close to reaching the total biomass of squid in California. The California sardine (*Sardinops sagax*) fishery collapsed in the 1960s, and a twenty-year moratorium was required before there was recovery to a fraction of prior spawning biomass (Wolf, 1992). Whether over-fishing or large scale, multidecadal climatic regime shifts caused this collapse is matter of debate (Chavez et al., 2003), but without an effective management plan, squid will continue to be fished because of market demand. Markets are driven by economic forces and traditionally do not control themselves in a biologically sustainable manner. A full recovery of the squid fishery occurred from 1998 to 2000 and thus spanned four generations of squid given a 6–9 month lifecyle; for the California sardine (with a 6-8 year lifecycle), a proportionally similar recovery period would be 24–32 years (Parrish[7]).

In 1998–99 the fishery for *Loligo opalescens* decreased to low levels during the El Niño event, then recovered to record levels in the following years. This was most likely due to the plasticity of squid development in relation to water temperature and upwelling and the short (4–6 month) life span of squid. One should not assume that the ability of this species to recover from environmental stress like El Niño applies also to the recent anthropogenic stresses associated with increasing fishery capacity. It remains to be seen if the large decline in southern California landings in the last five years (119,780–24,449 tons/year) is due to the small El Niño of 2002–03, the climate-regime shift in 1998, overfishing, or some other factor such as increased water stratification due to global warming. Although the short-lived squid may not be able to recover from overexploitation in short order, the huge number of long-lived birds, fish, and marine mammals (Morejohn et al., 1978; Lowry and Carretta, 1999) that depend on squid as a key forage species may not be able to recover rapidly from lack of management foresight. The recent establishment of the marine reserve system in the Channel Islands eliminates 13% of key squid fishing grounds. This ecosystem-based management approach may assist in protecting not only the squid but also their predators.

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Acknowledgments

This research was funded by a California Fish and Game award (no. FG7334MR) and a Coastal Environmental Quality Initiative Program grant (no. 783828-KH-19900) and was supported in part by the David and Lucile Packard Foundation through the Monteray Bay Aquarium Research Institute. Bruce Robison, Rich Ambrose, Peggy Fong, and Dick Zimmer provided thoughtful reviews. Andrea Steinberger assisted with data management.

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Variability in supply and cross-shelf transport of pink shrimp (*Farfantepenaeus duorarum*) postlarvae into western Florida Bay

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Abstract—The variability in the supply of pink shrimp (*Farfantepenaeus duorarum*) postlarvae and the transport mechanisms of planktonic stages were investigated with field data and simulations of transport. Postlarvae entering the nursery grounds of Florida Bay were collected for three consecutive years at channels that connect the Bay with the Gulf of Mexico, and in channels of the Middle Florida Keys that connect the southeastern margin of the Bay with the Atlantic Ocean. The influx of postlarvae in the Middle Florida Keys was low in magnitude and varied seasonally and among years. In contrast, the greater postlarval influx occurred at the northwestern border of the Bay, where there was a strong seasonal pattern with peaks in influx from July through September each year. Planktonic stages need to travel up to 150 km eastward between spawning grounds (northeast of Dry Tortugas) and nursery grounds (western Florida Bay) in about 30 days, the estimated time of planktonic development for this species. A Lagrangian trajectory model was developed to estimate the drift of planktonic stages across the SW Florida shelf. The model simulated the maximal distance traveled by planktonic stages under various assumptions of behavior. Simulation results indicated that larvae traveling with the instantaneous current and exhibiting a diel behavior travel up to 65 km and 75% of the larvae travel only 30 km. However, the eastward distance traveled increased substantially when a larval response to tides was added to the behavioral variable (distance increased to 200 km and 85% of larvae traveled 150 km). The question is, when during larval development, and where on the shallow SW Florida shelf, does the tidal response become incorporated into the behavior of pink shrimp.

Manuscript submitted 16 September 2003 to the Scientific Editor's Office.
Manuscript approved for publication 30 June 2005 by the Scientific Editor.
Fish. Bull. 104:60–74 (2006).

Patterns of recruitment of coastal species are highly variable, mainly because of the complex interaction of biotic and abiotic factors across the different life history stages. These factors include but are not limited to reproductive dynamics, larval dispersal and behavior, physiological tolerances, and the hydrometeorological regime in which their life stages develop (e.g., Shanks, 1995; Cowen, 2002). The commercially valuable tropical penaeid shrimps that use different habitats during their life cycle (offshore spawning grounds and estuarine nursery habitats) have to cope with a large suite of physical processes and stimuli (Rothlisberg et al., 1995, 1996). The pink shrimp (*Farfantepenaeus duorarum*) of Dry Tortugas is one of the most economically and ecologically important species in southwest Florida. The pink shrimp supports an important year-round fishery of about 4000 metric tons in an area of 10,000 km^2 between Dry Tortugas and Key West (Iversen et al., 1960; Klima et al., 1986). The Tortugas fishery is directly dependent on young shrimp that migrate from inshore nursery areas onto the offshore fishing grounds (Sheridan, 1996; Browder et al., 2002). Recruitment shows no relationship to spawning size; therefore harvest fluctuations are apparently due to environmental conditions rather than fishing operations (Nance and Patella, 1989). To effectively manage this species, it is necessary to have accurate information on the processes linking nursery and spawning ground populations.

Pink shrimp population dynamics are affected by physical processes and environmental conditions occurring in the southwestern (SW) Florida Shelf of the Gulf of Mexico, the Atlantic coastal zone, and the Florida Bay. Early research on gonad development (Cummings, 1961), distribution of larval stages (Jones et al., 1970), and analysis of length frequency distributions of fishery stock data (Iversen et al., 1960; Roberts, 1986) indicated that the center of spawn-

ing is northeast of the Dry Tortugas. If gravid females spawn northeast of the Dry Tortugas, larvae need to travel up to 150 km to reach the main nursery ground in western Florida Bay. Females spawn on the continental shelf at about 30 m of depth, where larvae develop, passing through several changes in feeding habitats, behavior, and physical stages (nauplii, zoeae, myses) (Dobkin, 1961; Ewald, 1965; Jones et al., 1970). Postlarvae undergo between three and eight additional planktonic stages before settlement. Larvae develop rapidly, needing only about 30 days to become postlarvae ready to settle to the bottom (Ewald, 1965; Dobkin, 1961). Planktonic stages (larvae and postlarvae) approach the coast and postlarvae enter the nursery grounds of Florida Bay at about 9–10 mm total length (Tabb et al., 1962; Allen et al., 1980; Criales et al., 2000). Larval development and ocean hydrodynamics must be tightly linked to successfully bring these planktonic stages to their coastal nursery grounds.

Mechanisms of transport used by planktonic stages of penaeid shrimps are highly variable, depending on the species, different environmental conditions, oceanic physical processes, and complexity of larval behaviors (e.g., Dall, 1990; Rothlisberg et al., 1995, 1996; Wenner et al., 2005). Physical oceanographic processes significantly affect the transport of planktonic stages from spawning to nursery grounds (Yeung and Lee, 2002; Criales et al., 2003). Two main immigration routes have been hypothesized for pink shrimp postlarvae entering Florida Bay: 1) postlarvae may drift south-southeast downstream with the Florida Current and enter Florida Bay through the tidal channels of the Lower and Middle Florida Keys (Rehrer et al., 1967; Munro et al., 1968), and 2) postlarvae may move northeast across the SW Florida shelf and enter the Bay at its northwestern boundary (Jones et al., 1970; Criales and Lee, 1995). The most widely recognized pathway for postlarvae to reach Florida Bay up-to-now has been by transport up the Atlantic side through the tidal channels of the Middle Florida Keys (Munro et al., 1968; Criales and McGowan, 1994; Criales et al., 2003). The favorable Ekman transport generated by the southeastern winds along the west-east oriented coast, and coastal countercurrent flow generated by cyclonic eddies provide favorable onshore transport mechanisms along the Florida Keys coast (Criales and Lee, 1995; Lee and Williams, 1999). In contrast, larval transport across the broad, shallow SW Florida Shelf has not been well studied and questions exist about the feasibility of this pathway. Subtidal frequency flows are weak in the SW Florida shelf and mainly in the alongshore (north-south) direction as a direct response to wind events (Koczy et al., 1960; Weisberg et al., 1996; Lee et al., 2001). Tidal currents are strong mainly in the cross-shelf direction (Wang, 1998; Smith, 2000). Freshwater discharges from the Everglades affect a broad area of the SW Florida shelf (Lee et al., 2001; Jurado, 2003). Isopleths less than 32 are typically confined to the region between Cape Sable and Cape Romano, and from 32 to 36 extend from near Cape Romano to the vicinity of Dry Tortugas in a highly variable annual pattern (Lee et al., 2001; Johns and Szymanski[1]).

For tropical penaeid shrimps that undergo larval development offshore, but whose nursery grounds are inshore, migratory behavior is a key factor for their advection to nursery grounds (Dall et al., 1990; Shanks, 1995). The simplest migratory behavior is vertical movement, and three types of vertical migrations are known to mediate horizontal transport of larvae: ontogenic, diel, and tidal (for reviews see Sponaugle et al., 2002). For some Australian penaeid species (banana prawn [*Fenneropenaeus merguiensis*], grooved tiger prawn [*Penaeus semisulcatus*], and eastern king prawn [*Melicertus plebejus*]) it has been shown that early planktonic stages (protozoeae and myses) perform diel vertical migration cued by light and that later in development (as postlarvae) the migration is cued by tides (Rothlisberg, 1982; Rothlisberg et al., 1983, 1995) and there is no cross-shelf displacement of larvae during the 15 days of diel behavior. Previous studies of pink shrimp in South Florida have clearly indicated ontogenic behavior for pink shrimp; postlarvae have a higher degree of mobility than earlier protozoeae and myses (Temple and Fischer, 1965; Eldred et al., 1965; Jones et al., 1970; Criales and Lee, 1995). On the other hand, diel behavior is not so well determined. Although protozoeae, myses and postlarvae were more abundant at the surface during the night than during the day, day and night differences have not been statistically significant in any of these previous studies. The effect of diel, tidal, or ontogenic combinations of behavior on cross-shelf transport from South Florida spawning grounds to western Florida Bay nursery grounds has not previously been explored. The postlarvae of many penaeid shrimps, including pink shrimp, are known to synchronize vertical migration with the tides at the entrance to estuarine nursery grounds (for reviews see Garcia and Le Reste 1981, Dall et al., 1990). This process is known as selective tidal stream transport (STST) (Forward and Tankersley, 2001). Penaeid postlarvae ascend in the water column during the flood and sit on the bottom during the ebb to maximize up-estuary movement (e.g., Rothlisberg et al., 1995). This behavior has been shown for pink shrimp postlarvae inside Florida Bay (Tabb et al., 1962; Roessler and Rehrer, 1971), but not along the border of the bay with the Gulf of Mexico. When during the life cycle and where on the shelf this tidal behavior begins and what the environmental cues are—these questions remain unanswered.

The purpose of our research was 1) to determine patterns of supply of pink shrimp postlarvae into Florida Bay through two distinct regions, 2) to define the most important transport route for planktonic stages from the Dry Tortugas into Florida Bay, 3) to examine alternative behavioral responses of larvae and postlarvae, and 4) to propose a recruitment mechanism for

[1] Johns, E., and D. Szymanski. 2003. Mixing it up in Florida Bay. Florida Bay News, summer 2003:1–3.

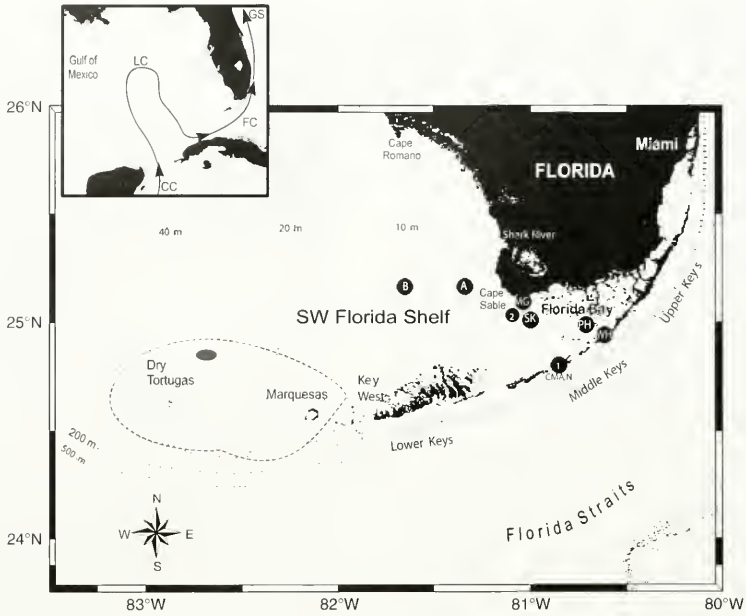

Figure 1

Map of the study area (with bathymetry) showing the channel net sampling stations at the northwestern and southeastern borders of the nursery grounds of Florida Bay, ADCP moorings, and CMAN and COMP stations. The Tortugas fishing grounds (area enclosed by dashed line) includes the center of spawning for *Farfantepenoeus duorarum* (filled ellipse). Northwestern stations: MG=Middle Ground and SK=Sandy Key; Florida Key stations: WH=Whale Harbor and PH=Panhandle; A and B=onshore and offshore ADCP moorings respectively; 1=Long Key CMAN station; 2=NW Florida Bay COMP station. Small map at the left corner indicates major currents in the Gulf of Mexico and off the coast of Florida. CC=Caribbean Current; LC=Loop Current; FC=Florida Current; GS=Gulf Stream.

pink shrimp across the SW Florida shelf that combines the effect of hydrodynamics with larval behavior. Four modes of behavior-related transport were simulated under hydrodynamic conditions occurring on the SW Florida shelf in order that the resulting distances traveled under each condition might be contrasted.

Material and methods

Pink shrimp postlarvae were collected in two regions of Florida Bay to evaluate postulated hypotheses of eastern and western gateways and pathways of larval transport into the bay. The two study sites consisted of two large channels connecting northwestern Florida Bay with the SW Florida shelf of the Gulf of Mexico (Sandy Key Channel [SK], and Middle Ground [MG]); and of more confined tidal channels in the Middle Florida Keys that connect the Bay with the Atlantic Ocean (Whale Harbor [WH], and Panhandle Key [PH]) (Fig. 1). Adjacent mud banks that are occasionally exposed at low tide and over-topped at higher tide stages define these channels. The averaged depth, tidal flow, and cross sectional area of the four channels are summarized in Table 1 to show the different levels of water flow through these pathways. Channels depths are similar, but western channels (Middle Ground and Sandy Key) have higher tidal flows and larger cross sectional areas than the Florida Keys channels (Table 1). Tidal fluctuations are primarily semidiurnal at all stations and have weaker diurnal constituents (Smith, 1998, 2000). Acoustic Doppler velocity meters (ADVMs) that measure continuous velocity and depth (tide and stage) and associated CTD instruments that measure conductivity and temperature were installed at each channel in January 2002. A boat-mounted acoustic Doppler current profiler (ADCP) was used to calculate total discharge across the cross-section of the channel during monthly sampling (Hittle et al., 2001).

Postlarvae were collected monthly in each channel during two nights around the new moon from January 2000 to December 2002. At the PH station sampling began in June 2000 after the original site (Captain Key channel) was abandoned because it had insufficient water flow for effective sampling. Two moored subsurface channel nets (net 1 and net 2) of 0.75-m^2 opening, 1-mm mesh size, and 500-μm mesh in the codend were suspended with floats at 0.5 m depth. Nets were deployed each night before dusk and removed shortly after dawn each day. General Oceanic flowmeters (2030R16, Low Speed Rotor, Miami, FL) were mounted in the mouth of the nets and the volume of water filtered through the nets was calculated for each net. *Farfantepenaeus duorarum* postlarvae were sorted, identified, and preserved in 90% ethanol. The raw catch in each sample was standardized to numbers of postlarvae per 1000 m^3 of water filtered. The average number of postlarvae over the two sampling nights was used as the mean monthly concentration for each net. The average of monthly postlarval concentration for each region (northwestern Florida Bay *vs.* Florida Keys) was compared by using a nonparametric two-way analysis of variance (ANOVA) (Anderson, 2001).

Three 12-hour experiments were conducted in summer 2002 in the SK channel to document the behavioral response of pink shrimp postlarvae to ebb and flood tides. Consecutive pairs of night (i.e. dark) flood and dark-ebb plankton samples were taken hourly from 19:00 to 07:00 h from 9 to 10 July (new moon), 23 to 24 July (full moon), and 8 to 9 August (new moon). In addition, plankton samples were taken for 10 consecutive hours daily on 8 August to verify the response of postlarvae to light. The nonparametric Kruskal-Wallis test and analysis of variance (ANOVA) were used to determine differences in concentration of postlarvae between dark-ebb and dark-flood periods.

To evaluate the possible effect of environmental variables on larval supply to Florida Bay and the pattern of seasonality in postlarval concentrations, available time series of winds and sea surface temperature (SST) on the coastal shelf were examined in relation to our time series of monthly measured larval concentrations. In particular we were looking for a pattern that might help to determine the reason for the marked summer peak in the concentration of postlarvae at the western border of Florida Bay. Time series of hourly winds and sea surface temperature (SST) for the 3-year sampling period were obtained from the Coastal Marine Automated Network (CMAN) station at Long Key, and from the Coastal Ocean Monitoring and Prediction System (COMP) station in NW Florida Bay (Fig. 1). Temperature and wind time series from the Long Key CMAN station and the NW Florida Bay COMP station were highly correlated with each other (r^2=0.9; P<0.01). The longer Long Key time series were used for coastal SST and wind analysis. Wind speed and direction over the Keys, as measured at CMAN sites, are highly coherent (Peng et al., 1999) and useful for explaining currents on the SW shelf (Lee and Williams 1999). Monthly averages of wind vectors and SST were calculated from hourly CMAN time series data (years 2000 to 2002) to examine the effect of winds and SST on the monthly postlarval collections.

Table 1

Mean cross section depth, peak tidal flow, and cross section area of the four channels sampled for pink shrimp (*Farfantepenaeus duorarum*) postlarvae at the northwestern border of Florida Bay, Middle Ground (MG) and Sandy Key (SK), and at the southeastern edge in the Middle Florida Keys, Whale Harbor (WH), and Panhandle Key (PH). Area was calculated at zero (m) of mean sea level.

Station	Depth (m)	Peak tidal flow (m^3/sec)	Cross area (m^2)
MG	3.0	1420	2723
SK	3.1	570	1345
WH	3.3	280	407
PH	2.0	30	74

Time series of current data from two established stations with moored ADCPs and temperature and salinity sensors were used to drive our transport model. Initially, these data were examined to determine whether prevailing currents alone could explain the transport of larvae from the Tortugas spawning grounds to Florida Bay nursery grounds. These stations also were a source of salinity data used in one set of simulations. These stations were located on the inner SW shelf of the Gulf of Mexico, about 30 km from our MG station (Lee et al., 2001) (Fig. 1). This array monitored coastal currents as part of the Florida Bay Circulation and Exchange Study (Lee et al., 2001). The ADCP moorings were located at depths of 6.4 m (mooring A=onshore) and 11.6 m (mooring B=offshore) and recorded data every 30 minutes for a 3-year period (A=21 September 1997 to 15 October 2000; B=22 September 1997 to 17 October 2000). The two ADCP moorings were about 30 km apart. Lee et al. (2001) reported insignificant differences between currents in the vertical for cross-shelf transport in the shallow SW Florida shelf. Wind and current vectors were resolved into cross-shelf (u=east [+] and west [−]) and alongshore (v=north [+] and south [−] constituents). The east-west and north-south displacement of current and wind constituents (half-hour current data and the hourly wind data) was the product of each current and wind constituent by the respective time interval. Correlation analysis was conducted on currents and wind time series.

A harmonic analysis was conducted on the three-year ADCP raw data to define tidal constituents and current magnitude. Period (Pi) and tidal excursion (Ti) were calculated for each constituent from amplitudes (Ai) and frequencies of the constituents as follows:

$$Ti = AiPi/\pi.$$

A simple Lagrangian trajectory model was developed to estimate the drift of planktonic stages. The model used the observed currents at ADCP moorings A and B to calculate trajectories. Because of the lack of information on spatial current variations and the difficulty of extrapolating vertical current profiles from one depth and bottom relief to other conditions, a simple two-dimensional (horizontal) simulation model was used. For the computations we selected the highest bin from the ADCP that had good data throughout the tidal cycle at each station. This bin typically was 1 m below the mean water level at that location and was the highest bin not affected by instrument sidelobe interference. Because instantaneous bottom currents were closely aligned in direction with surface currents and because magnitudes were only 25% lower, the tidal currents were barotropic and we used, therefore, the surface currents to estimate the largest possible distance traveled.

The larval transport was calculated with the equation

$$dx_i/dt = u_i,$$

where x_i = position vector of the larvae;
t = time; and
u_i = the local current velocity.

An Euler (forward in time) integration rule was used to numerically solve this equation. Because only two ADCPs (A and B) provided the current data for this large region, no attempt was made to extrapolate a current field from them. Simulations were run by using current meters A and B independently and by assuming that the current field was spatially homogeneous. The trajectories therefore were two-dimensional in the horizontal plane and the result was identical to a progressive vector diagram. Comparison between the two sets of trajectories (A and B) provided an estimate of the possible variability. The model was used to explore the potential transport of planktonic stages under various assumptions of behavior controlled by environmental cues: 1) a behavioral response to salinity and light, 2) a diel behavior, 3) a diel and tidal behavior throughout the planktonic phase, and 4) an ontogenic change that began with diel behavior and added a tidal behavior at the 15th day. All four hypotheses of larval behavior in relation to transport were simulated in order that their effects on distance traveled could be compared and contrasted. In all simulations, we assumed that larvae traveled only at night. We also assumed that the source of the pink shrimp larvae was located immediately northeast of the Dry Tortugas about 150 km from western Florida Bay (Cummings, 1961; Jones at al., 1970; Roberts, 1986). The program simulated distances traveled by particles for a period of 30 days (e.g., days 1–30, 31–60, 61–90, etc.), a period that corresponds to the estimated developmental period for pink shrimp from the time of hatching to the postlarval stage when larvae are ready for settlement (Dobkin, 1961; Ewald, 1965).

Results

Patterns of postlarval supply, SST, and winds

The monthly influx of postlarvae through the Middle Florida Keys channels (WH and PH) exhibited a highly variable temporal pattern from year to year. Postlarvae were observed every month through the three years (Fig. 2A). Peaks of postlarvae through the Middle Keys channels occurred in May, July, August, and October 2000; in January, July, and October 2001; and in January, March, June, and September 2002. In contrast, the monthly influx of postlarvae through the northwestern stations (SK and MG) showed a strong seasonal pattern with one distinct high peak centered in summer from July through September for each year of the 3-year period (Fig. 2B). The number of postlarvae entering through northwestern Florida Bay was much higher than through the Keys stations. The mean concentration of postlarvae per station over the 3-year period indicated that concentrations of postlarvae entering northwestern Florida Bay through SK and MG channels were about eight times greater than through the Florida Keys channels of WH and PH (Fig. 3). Results from a two-way ANOVA indicated that there was a significant effect of site (northwestern stations *vs.* Florida Key stations) and month on the supply of postlarvae entering Florida Bay (Table 2).

Winds showed a seasonal pattern; the spring and summer were dominated by weak southeasterly winds and the fall and winter, by strong northerly winds (Fig. 2, C–D). The monthly average alongshore showed a weak northward constituent in spring–summer of each year (Fig. 2C). The monthly average cross-shelf winds were consistently negative (toward the west) and showed no seasonality (Fig. 2D). The average temperature over the three-year time series was 26.1°C, and winter temperatures in 2000–01 were lower than in 2001–02 (Fig. 2E). In summer, during the period of peak postlarval immigration through the northwestern stations (MG and SK), the alongshore wind constituent was mainly northward, the cross-shelf wind was westward, and the SST was above average during the three-year period (Fig. 2, A–E). Postlarval concentrations at the northwestern stations were correlated with SST and alongshore winds (Fig. 2, B–E; Table 3). Postlarval concentrations at the Florida Keys stations (WH and PH) were not correlated with either winds or SST.

Subtidal and tidal currents at the SW Florida shelf

Advective displacement derived from two ADCP velocity records indicated that the net current is primarily in the alongshore direction (Fig. 4, A and B). The alongshore flow from onshore mooring A was northward, had a total mean velocity of 0.0062 m/sec, and a total water displacement of 589.3×10^3 m over the three years (Fig. 4A). The cross-shelf flow was westward, had a mean velocity of −0.0005 m/sec, and a total water displacement of -289.7×10^3 m. The alongshore flow from offshore moor-

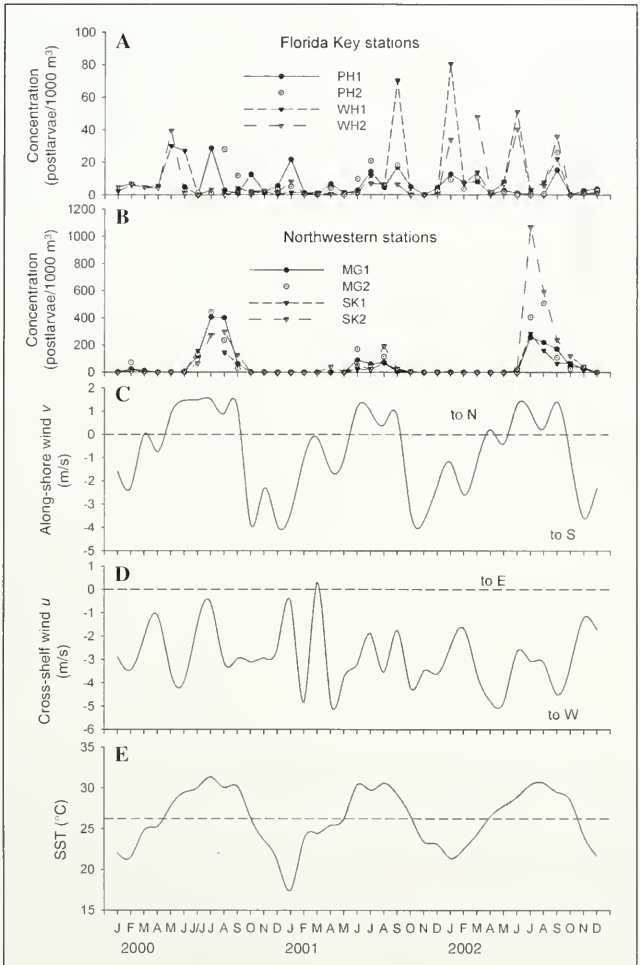

Figure 2

Monthly time series of pink shrimp (*Farfantepenaeus duorarum*) postlarval concentrations, winds, and sea-surface temperature: (**A**) mean concentration of pink shrimp postlarvae at the Florida Key stations of Whale Harbor (WH) and Panhandle (PH); (**B**) mean concentration of pink shrimp postlarvae at the northwestern Florida Bay stations of Middle Ground (MG) and Sandy Key (SK); concentrations of two nets are depicted as 1 and 2; (**C**) alongshore winds (v); (**D**) cross-shelf winds (u); (**E**) sea-surface temperature (SST). Winds and SST data are from Long Key CMAN station.

ing B was southward, had a mean velocity of −0.0038 m/sec and a total water displacement of -364.7×10^3 m (Fig. 4B). The cross-shelf flow was eastward, had a mean speed of 0.0015 m/sec, and a total water displacement of 145.5×10^3 m and a resultant southeastward current. The alongshore winds measured at Long Key were southward and had a total water displacement of 16.1×10^3 m, and the cross-shelf winds were westward and had a total

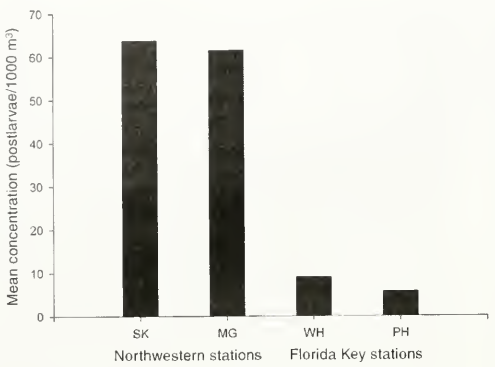

Figure 3

Mean concentration of pink shrimp (*Farfantepenaeus duorarum*) postlarvae over a three-year period at each sampling station: northwestern Florida Bay stations—Middle Ground (MG) and Sandy Key (SK); Florida Key stations—Whale Harbor (WH) and Panhandle (PH).

Table 2

Results of a nonparametric two-way ANOVA of the effect of site and month on pink shrimp (*Farfantepenaeus duorarum*) postlarvae entering Florida Bay. $P<0.05$ is indicated with an asterisk. SS=sum of squares; MS=mean of squares.

Factor	df	SS	MS	*F*	*P*
Month	80	756.7	9.5	5.6	0.007*
Site	1	65.9	65.9	39.3	0.002*
Month × site	1	1191.5	1191.5	711.3	0.007*
Error	461	772.2	1.7		

Table 3

Correlation coefficients of pink shrimp (*Farfantepenaeus duorarum*) postlarval concentrations with sea surface temperature (*SST*), cross-shelf wind (*U*), and alongshore wind (*V*) at the four sampling stations of MG= Middle Ground, SK= Sandy Key, WH= Whale Harbor and PH= Panhandle. Environmental data are from Long Key CMAN station. Significant correlations ($P<0.05$) are indicated with an asterisk.

	SST	*U*	*V*
MG	0.82*	−0.025	0.67*
SK	0.73*	0.11	0.57*
WH	0.15	0.16	0.36
PH	−0.17	0.14	−0.09

water displacement of -86.3×10^3 m (Fig. 4C). The subtidal currents in this region are very weak as also observed by other investigators (Koczy et al., 1960; Rehrer et al., 1967). Correlation coefficients between winds and currents in the alongshore direction (*v*) were significant for both onshore and offshore currents time series (Table 4). Correlation coefficients between winds and currents in the cross-shelf direction were higher in the onshore than in the offshore data series. This analysis indicated that prevailing currents, overall, were not favorable to passive transport of larvae from the Tortugas to western Florida Bay.

A harmonic analysis of the 3-year ADCP data showed that semidiurnal tidal constituents (M_2, S_2, K_2, and N_2, see Table 5 for explanation of abbreviations) are dominant on the SW Florida shelf. M_2 was the strongest tidal constituent and its east-west constituent explained 95% of the total current variance. The east-west amplitude of the M_2 constituent was 0.32 m/s for both moorings, and the north-south was 0.07 m/s for mooring A and 0.04 m/s for mooring B. The east-west amplitude (0.32 m/s) was much stronger than the long-term averaged subtidal cross-shelf constituent at both stations (0.001 m/s). The east-west tidal excursion of the M_2 constituent was similar for both moorings, but a few meters larger on the offshore station (Table 5). This result indicates that it is reasonable to consider that there are similar tidal excursions on the SW shelf up to 50 km.

Ebb versus flood catches

Concentration of postlarvae collected hourly over a complete dark portion of a tidal cycle showed clearly that dark-ebb catches were negligible (<10%) by comparison with dark-flood catches (>90%) (Fig. 5, A–C). Hourly concentrations of postlarvae collected on the dark flood were 92.7% from 9 to 10 July, 90.2% from 23 to 24 July, and 86.9% from 8 to 9 August 2002. A nonparametric Kruskal-Wallis test showed significant differences in catches of postlarvae between dark-ebb and dark-flood periods (Kruskal-Wallis: $H=15.5$, $n=36$, $P<0.001$; (ANOVA: $F=18.6$; $P<0.001$). Samples taken during the day on 8 August confirmed the hypothesis that postlarvae are present mostly at night in the water column (Table 6). A total of 18 postlarvae (31.5 postlarvae/1000 m^3) were captured during 10 consecutive daylight hours, against 2657 (3702.5 postlarvae/1000 m^3) captured during 10 consecutive hours of darkness. Although concentrations of postlarvae tend to increase with the tidal current, these differences were not significant (Kruskal-Wallis: $H=10.3$, $n=36$, $P=0.5$). From 9 to 10 July, no postlarvae were captured during the hours of highest current speed (2:00 to 3:00 h), which coincided with high rain and winds (Fig. 5A). It is not clear whether these factors caused a change of behavior in the postlarvae or a malfunction of the net. From 23 to 24 July, concentration of postlarvae on the dark flood followed the cur-

rent speed; highest catches occurred at the maximum speed and lowest catches at the minimum speed (Fig. 5B). From 8 to 9 August, the highest peak of postlarvae occurred at the end of the dark-flood period when the current had decreased in speed (Fig. 5C).

Transport simulations

Results of channel net sampling showed that the greatest postlarval influx occurred at the northwestern border of the bay, where there was a strong seasonal pattern with maxima from July through September each year. Postlarval concentrations at the northwestern stations were correlated with the alongshore winds and with surface temperature but did not correlate with the cross-shelf winds. However, postlarvae need to travel up to 150 km across the shelf to reach their nursery grounds.

Cross-shelf transport mechanisms were explored by using a Lagrangian trajectory model that simulated the maximum distance traveled by planktonic stages moving at night for a 30-day period. Four scenarios of transport were modeled under different assumptions of behavior:

Scenario 1 With the assumption that planktonic stages (larvae and postlarvae) of pink shrimp respond to light and salinity changes (Hughes 1969a, 1969b), the first simulation postulates that larvae and postlarvae move horizontally with a vertical migratory behavior cued by changes in salinity. Larvae and postlarvae swim to the surface at night when an increase in salinity is detected and remain near the bottom when the salinity decreases.

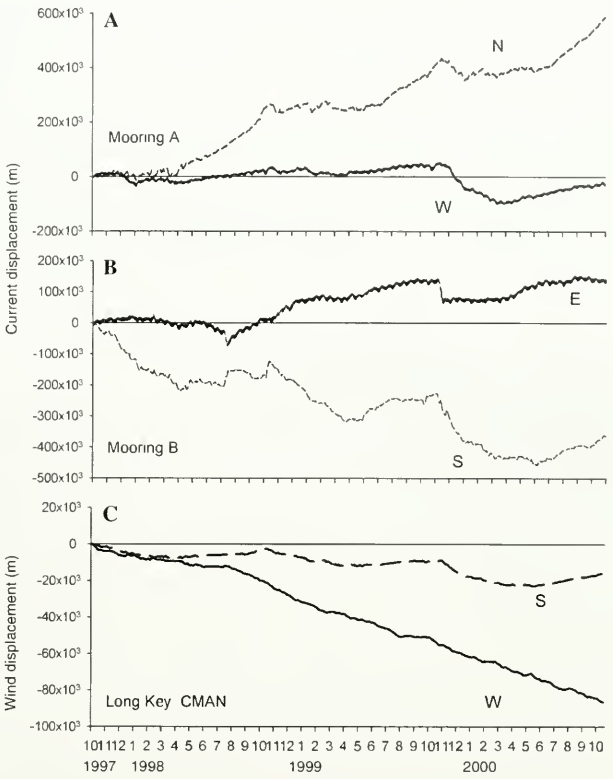

Figure 4

Time series of current and wind displacement, October 1997–October 2000. Current data are from two ADCPs located at the SW Florida shelf, and wind data are from Long Key CMAN station; (A) onshore ADCP mooring A, (**B**) offshore ADCP mooring B; see ADCP locations in Figure 1. (**C**) Wind displacement. Alongshore constituents are represented by interrupted lines (N=north [+], S=south [−]) and cross-shelf by continuous lines (E=east [+], W=west [−]).

Onshore mooring The maximum distance traveled in the cross-shelf direction was 98 km eastward and 70% of larvae traveled up to 30 km (Fig. 6A). The average eastward distance in all simulations was 22 km. The maximum displacement occurred in fall-winter. Alongshore distances were as much as 25 km northward (70% of larvae) and 15 km southward (30%) (Fig. 6, A and B).

Offshore mooring The maximum distances traveled in the cross-shelf direction was 100 km (84% of larvae traveled 40 km). Alongshore distances were as much as 15 km northward (70%) and 20 km southward (30%) (Fig. 6, C and D).

Scenario 2 The second simulation assumes that planktonic stages travel at night using the instantaneous current.

Onshore mooring Distances traveled in the cross-shelf direction reached a maximum of 68 km and 75% of larvae traveled only 30 km eastward (Fig 6A). The average eastward distance in all simulations was 15 km. The maximum displacement occurred in spring-summer (May to September 1998) during the first year and in fall-winter (October 1999 to February 2000) during the second and third year. Distances recorded in the alongshore direction were as far as 40 km northward (48% of larvae) and 30 km southward (52%) (Fig. 6, A and B).

Offshore mooring Maximum distance traveled in the cross-shelf direction reached 60 km eastward and 80% of larvae traveled less than 30 km. Distances recorded in the alongshore direction were as far as 40 km northward (51%) and 40 km southward (49%) (Fig. 6, C and D).

Scenario 3 Under the assumption that pink shrimp larvae and postlarvae migrate vertically in a tidal cycle, the third simulation postulates that larvae and postlarvae swim in the water column near the surface at night during the flood tide and remain near the bottom during the ebb tide. In this simulation it is assumed that planktonic stages move by using the eastward current (flood tide) during the postulated 30 days of larval development.

Onshore mooring The maximum distance traveled in the cross-shelf direction was 200 km eastward and 86% of the larvae exceeded 150 km. The average eastward distance in all simulations was 132 km. The maximum larval displacement occurred from December 1999 through March 2000. Distance traveled in the alongshore direction was 45 km northward (70%) and 5 km southward (30%) (Fig. 6, A and B).

Offshore mooring The maximum larval displacement in the cross-shelf direction was 200 km eastward and 85% of the larvae reached 150 km. The maximum eastward displacement occurred in fall and in winter. Distance traveled in the alongshore direction was as much as 40 km northward (82%) and 5 km southward (18%). The maximum distance traveled was recorded in March–April and June 2000 (Fig. 6, C and D).

Scenario 4 In this simulation, it is assumed that there is a change in behavior for pink shrimp larvae—an assumption similar to the one taken in simulations for some Australian penaeid species (Rothlisberg, 1982; Rothlisberg et al., 1995, 1996). Early larval stages (protozoea and myses) migrate vertically in a diel cycle and there is no cross-shelf displacement during the first 15 days of development. Later in development, postlarvae migrate by using tidally induced behavior superimposed on the diel behavior for the remaining 15 days of planktonic development, and the eastward current (flood tide).

Onshore mooring The maximum displacement of larvae in the cross-shelf direction was 100 km eastward

Table 4

Correlation coefficients of wind and current components. U and V are the east-west and north-south components respectively. Nearsurface currents are from onshore (A) and offshore (B) ADCP moorings over the SW Florida shelf. Wind data are from Long Key CMAN station. Significant correlations ($P<0.05$) are indicated with an asterisk.

	Mooring A		Mooring B	
	onshore		offshore	
	U-current	V-current	U-current	V-current
U-wind	−0.25*	−0.22*	−0.10	−0.06
V-wind	0.26*	0.55*	0.12	0.60*

Table 5

Harmonic analysis results conducted on three years of ADCP data (September 1997–October 2000). Moorings were located at the SW Florida shelf: A (onshore) and B (offshore) moorings. U and V are the east-west and north-south tidal consistuents, respectively. Explained variance of constituent U was 95% and of V was 50% (for A), and 96% and 29% (for B), respectively. M2=semidiurnal lunar; S2= semidiurnal solar; N2=semidiurnal larger lunar elliptic; K1-diurnal lunisolar; M1=diurnal smaller lunar elliptic; O1=diurnal principal lunar; K2=semidiurnal lunisolar.

			Tidal constituent U		Tidal constituent V	
	Tidal constituent	Period (h)	Amplitude (m/sec)	Tidal excursion (m)	Amplitude (m/sec)	Tidal excursion (m)
A	M2	12.42	0.321	4561.7	0.070	993.5
	N2	12.66	0.056	810.8	0.013	191.5
	S2	12.00	0.100	1368.2	0.017	239.3
	K1	23.93	0.049	1332.9	0.015	408.7
	M1	24.84	0.005	139.5	0.001	31.3
	O1	25.82	0.039	1139.1	0.010	289.9
	K2	11.97	0.025	345.6	0.010	135.8
B	M2	12.42	0.323	4593.0	0.038	539.4
	N2	12.66	0.057	828.3	0.007	105.9
	S2	12.00	0.105	1439.7	0.009	129.3
	K1	23.93	0.052	1434.4	0.008	213.9
	M1	24.84	0.003	93.9	0.002	54.1
	O1	25.82	0.043	1278.1	0.002	68.0
	K2	11.97	0.023	319.5	0.005	63.1

and 86% of larvae reached 80 km. The average eastward distance traveled in simulations was 66 km. The maximum distances traveled in the alongshore direction was 25 km northward (70% of larvae) and 10 km southward (30%). The maximum distance traveled was recorded in March–April and June 2000 (Fig. 6, A and B).

Offshore mooring The maximum displacement of larvae in the cross-shelf direction was 90 km eastward and 85% of larvae reached 80 km. Distance traveled in the alongshore direction reached 20 km northward (86% of larvae) and 5 km southward (14%) (Fig. 6, C and D).

Discussion

The monthly influx of pink shrimp postlarvae entering Florida Bay through its northwestern border showed a strong seasonal pattern of annual high peaks in summer over the 3-year period. Postlarval concentrations were correlated with alongshore winds and sea surface temperature. Alongshore winds were seasonal, with a weak northward constituent in spring–summer of each year changing to a strong southward in fall and winter. This seasonal pattern agrees with the general circulation described for the SW Florida shelf, highly dependent on synoptic-scale winds, coupled with a strong seasonality and strong tidal currents (e.g., Weisberg et al., 1996; Wang, 1998; Smith, 2000; Lee et al., 2001). Although tidal currents seem to be the main vehicle of eastward transport for planktonic stages, alongshore winds may be fundamental for moving larvae northward along the SW Florida shelf by avoiding a drift with the Florida Current or with the cyclonic circulation of the gyres that form southwest of the Dry Tortugas (Lee et al., 1994; Fratantoni et al., 1998). Under these circumstances larvae may reach Florida Bay by the shortest route in summer using tidal currents and winds across the shallow SW Florida shelf and entering Florida Bay by its northwestern border. The summer seasonality of postlarval immigration may also be amplified by the seasonality of spawning because higher temperatures induce higher spawning activity (Cripe, 1994) and consequently more recruits to enter the Bay during favorable onshore conditions.

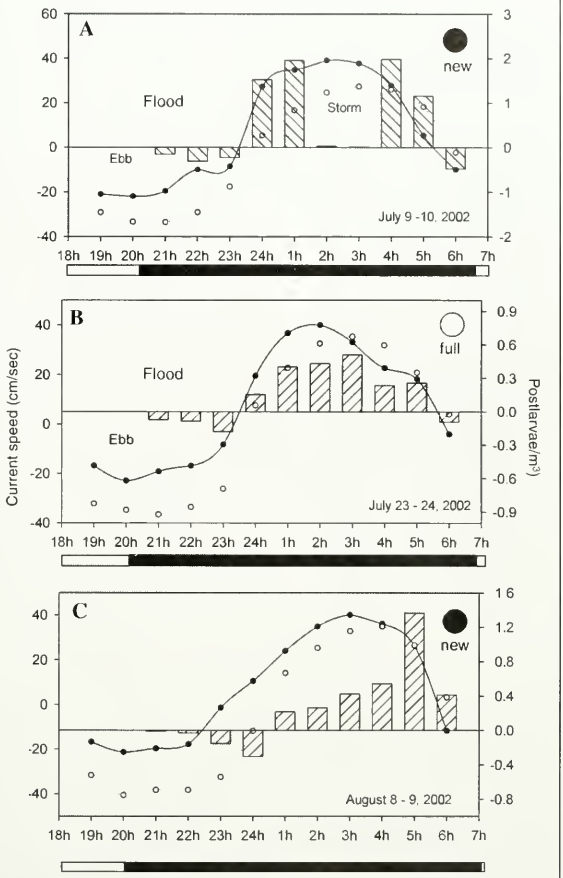

Figure 5

Hourly concentration of pink shrimp (*Farfantepenaeus duorarum*) postlarvae at Sandy Key station (SK) during a complete dark (night) tidal cycle conducted during (**A**) new moon, 9–10 July 2002, (**B**) full moon, 23–24 July 2002, and (**C**) new moon, 8–9 August 2002. Right *y*-axis indicates concentration of postlarvae/m^3; left *y*-axis is tidal current speed (cm/sec) measured by acoustic Doppler velocity meter (filled circle and solid line) and by flowmeter (empty circles and interrupted line). Positive values in the *y*-axes indicate transport into Florida Bay (flood), and negative values transport out of the Bay (ebb). Horizontal bars on the bottom indicate hours of darkness versus light.

Another alternative explanation for the summer larval immigration is that larvae may take advantage of a distinct annual tidal cycle produced in summer every year as a result of the interaction of the periods of the diel vertical migration and the tidal constituent (S_2, K_1) with the annual cycle of the length of the night (Criales et al., 2005). Larvae moving vertically in the water column with a diel behavior can be transported up to 70 km onshore in summer because the eastward current of the tidal constituents matches the diel cycle over extended intervals in the shorter summer nights

Table 6

Data from ebb-flood experiment conducted at Sandy Key (SK) station during 20 consecutive hours. E=ebb, F=flood, L=light, D=dark. VWF = volume of water filtered.

Date	Collection time	Tide stage	Light vs. dark	VWF (m^3)	Number of postlarvae	Concentrations (postlarval m^3)
08/08/2002	11:00	E	L	395.8	7	17.7
08/08/2002	12:00	E	L	535.3	2	3.7
08/08/2002	13:00	F	L	1360.1	0	0.0
08/08/2002	14:00	F	L	1262.3	0	0.0
08/08/2002	15:00	F	L	971.3	8	8.2
08/08/2002	16:00	F	L	531.2	1	1.9
08/08/2002	17:00	F	L	0.0	0	0.0
08/08/2002	18:00	F	L	0.0	0	0.0
08/08/2002	19:00	E	L	450.6	0	0.0
08/08/2002	20:00	E	L	575.6	0	0.0
08/08/2002	21:00	E	D	530.9	5	9.4
08/08/2002	22:00	E	D	477.6	14	29.3
08/08/2002	23:00	E	D	60.7	7	115.4
08/09/2002	0:00	E	D	263.3	87	330.4
08/09/2002	1:00	F	D	648.6	141	217.4
08/09/2002	2:00	F	D	944.3	247	261.6
08/09/2002	3:00	F	D	1164.1	491	421.8
08/09/2002	4:00	F	D	977.5	529	541.2
08/09/2002	5:00	F	D	737.8	1006	1363.6
08/09/2002	6:00	F	D	315.1	130	412.5

(Criales et al., 2005). Therefore, pink shrimp and other fish and invertebrate species that use tidal currents for transport with a daily vertical behavior may take advantage of this annual tidal cycle to improve their chances of reaching coastal nursery habitats.

The monthly influx of postlarvae through the Middle Florida Keys channels exhibited a highly variable seasonal pattern from year to year and from station to station. This section of the Keys coastal waters is frequented by coastal cyclonic eddies that originate at the Dry Tortugas and move downstream at 5–17 km/day along the edge of the shelf at intervals of 1 to 3 months (Fratantoni et al., 1998; Yeung et al., 2001). For planktonic stages, these eddies may serve as a delivery mechanism from offshore spawning grounds to the southeastern border of Florida Bay, allowing an onshore transport by the coastal countercurrent flow generated by the cyclonic circulation (Lee et al., 2001; Yeung et al., 2001; Criales et al., 2003). Episodic, mesoscale events associated with boundary current fronts and eddies may cause high variability in transport (Lee et al., 1994; Limouzy-Paris et al., 1997; Yeung and Lee, 2002). This variability was reflected in the influx of pink shrimp postlarvae through Middle Keys channels (Criales et al., 2003). The influx of postlarvae at WH and PH channels in the present study was also highly variable and there was no correlation with winds or sea surface temperature. Therefore, we hypothesized that the high variability in postlarval influx detected at the Florida Keys channels reflects the temporal and spatial variability associated with the passage of coastal eddies.

Simulations of transport based on current observations indicated that passive larvae could not consistently be advected the estimated 150 km eastward across the shelf between spawning and nursery grounds in 30 days. This is true primarily because of the weak eastern current and the reversing nature of tides. In contrast, planktonic stages (larvae and postlarvae) moving at night with the eastward current (flood tide) can consistently travel 100 to 200 km in 30 days. Hypothetically, 85% of the larvae can be transported far enough from the known spawning grounds of Dry Tortugas to the nursery grounds in western Florida Bay in 30 days. Previous works conducted inside Florida Bay (Tabb et al., 1962; Roessler and Rehrer, 1971) and our own data obtained along the western border of Florida Bay demonstrated the ability of pink shrimp postlarvae to respond to the dark flood tide and to distinguish between day and night. Over 90% of postlarvae were caught in the dark flood period and only a few postlarvae were caught during daylight hours. This behavior needs to be investigated for early larval stages to define the exact age at which larvae begin reacting to change in tides and to environmental cues that trigger the vertical movement in relation to tidal stage. For other penaeid

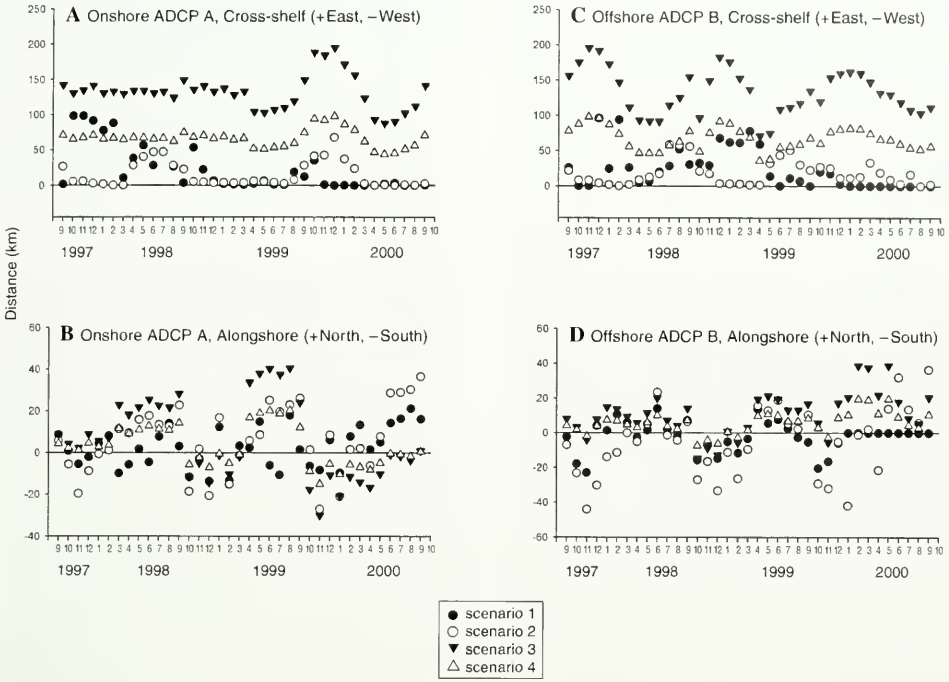

Figure 6

Outputs of transport simulations of pink shrimp (*Farfantepenaeus duorarum*) planktonic stages (larvae and postlarvae) developed from *in situ* current observations and under different scenarios of larval behavior. Each point represents 30 days of travel from September 1997 to October 2000; (**A** and **B**) outputs from onshore ADCP A currents, cross-shelf and alongshore constituents, respectively; (**C** and **D**) outputs from offshore ADCP B currents, cross-shelf and alongshore constituents, respectively. Scenario 1 (filled circles) = planktonic stages migrating with the instantaneous current and a diel behavior (at night) cued by changes in salinity; scenario 2 (empty circles) = planktonic stages migrating with the instantaneous current and a diel behavior (at night); scenario 3 (filled triangles) = planktonic stages migrating with a diel (at night) and a tidal (eastward current) behavior; scenario 4 (empty triangles) = planktonic stages migrating by an induced ontogenic change of behavior (a diel behavior during the first 15 days and a tidally induced behavior (eastward current) superimposed on the diel behavior (at night) for the remaining 15 days).

species (*Fenneropenaeus merguiensis, Penaeus plebejus,* and *Penaeus semisulcatus*) in the Gulf of Carpentaria, Australia, an ontogenic change in behavior has been documented for planktonic stages (Rothlisberg, 1982; Rothlisberg et al., 1995. 1996; Condie et al., 1999). Results of these studies showed that during the first two weeks of planktonic development, larvae migrate vertically in a diel cycle; later in development, the vertical migration is tidally induced. Under those conditions there was little or no systematic cross-shelf displacement of larvae during the first two weeks; afterward, cross-shelf displacement occurred rapidly (Rothlisberg et al., 1995; 1996). Simulation of transport for pink shrimp larvae using this ontogenic change of behavior indicated that planktonic stages can be transported up to 100 km eastward and 85% of larvae reach 80 km. If this behavior applies to pink shrimp, the location of the spawning grounds needs to be reconsidered in favor of areas closer to Florida Bay. Alternatively, the behavior of early planktonic stages may have been underestimated. Results of this research indicated once again the extreme importance of defining larval behavior and including behavior in dispersal models.

The cue(s) that penaeid postlarvae use to migrate in the water column during the flood tide and to return to the bottom on the ebb tide are not completely understood and could be species specific. Hughes (1969a, 1972) demonstrated in laboratory experiments that

pink shrimp postlarvae react to changes in salinity by changing swimming direction. Postlarvae were more active in the water column with increases in salinity, and this finding implies a shoreward displacement with the flood tide. Similar responses to salinity changes have been found for postlarvae of *Farfantepenaeus californiensis, Farfantepenaeus brevirostris, Litopenaeus stylirostris,* and *Litopenaeus vannamei* from the Mexican Pacific (Mair, 1980). The importance of a salinity cue for transport has been questioned for other penaeid species that inhabit hypersaline estuaries (southeast African, western Australia) in which penaeid postlarvae would need to move against a salinity gradient (Penn, 1975; Forbes and Benfield, 1986; Rothlisberg et al., 1995). Our simulations of transport guided by salinity changes indicated that planktonic stages could travel distances in the range of only 30 km in 30 days. This result may indicate that salinity is not the only environmental factor controlling long cross-shelf migrations of pink shrimp. However, Hughes (1969a, 1969b) in early experiments suggested that a salinity cue could apply to postlarvae near the nursery grounds. Changes in water pressure have been proposed as the only environmental factor that triggers the vertical migration of postlarval shrimps in the Gulf of Carpentaria, Australia (Penn, 1975; Forbes and Benfield, 1986; Rothlisberg et al., 1995). Laboratory experiments and numerical models have shown that tiger shrimps (*Penaeus semisulcatus* and *Penaeus esculentus)* larvae switch behavior when the change in water pressure with tides becomes a significant fraction of the total pressure (Rothlisberg et al., 1996; Condie et al., 1999; Vance and Pendrey[2]). This behavior only occurred in larvae above a certain size. However, it still remains to be determined whether, in a natural ecological context, the rates of relative changes of pressure are consistent with the tidal cycle periodicity and are detectable at absolute amounts in order to permit a behavioral response.

By means of simulations of transport, we have identified a potential STST mechanism for planktonic pink shrimp to migrate the estimated 150 km in 30 days from spawning to nursery grounds over the Florida shelf. Organisms inhabiting coastal ecosystems dominated by tides have the potential to control their cross-shelf movement through STST (Shanks, 1995). The extent of the transport depends on the speed of the tidal current and the time that organisms spend in the water column. Success in reaching the nursery grounds depends upon the stage in larval or postlarval development when the tidal behavior is added. A dependence on tidal currents for the entire larval transport period was postulated for *Melicertus latisultacus* in Western Australia (Penn, 1975). The shrimp *Lucifer faxoni* is the only species for which a STST mechanism across the shelf has been shown (Woodmansee, 1966). Strong tidal currents and several coastal sources of fresh water define the spawning grounds of the wide and shallow SW Florida shelf (Lee et al., 2001; Jurado, 2003). Under these conditions, parts of the SW Florida shelf may behave as an estuary in which planktonic pink shrimp may easily recognize tides by means of endogenous behavior or environmental variables.

From this study we determined that the greatest influx of postlarval pink shrimp occurred at the northwestern border of Florida Bay in summer. Postlarvae entering Florida Bay through the channels of the Middle Florida Keys occurred at a much lower magnitude and there were only sporadic peaks and no apparent seasonality in influx. The transport mechanism of planktonic stages of pink shrimp across the SW Florida shelf seems to depend heavily on semidiurnal tides and larval behavior, and much less on seasonal winds. The response of postlarvae to the tidal currents was clearly observed at the western margin of Florida Bay. Such behavior needs to be explored in early stages to define the age at which larvae begin to respond to tides, the location on the Florida shelf at which this response occurs, and the specific environmental cues linked to such behavior. With this information, more realistic simulations of transport can be made with a complete hydrodynamic model that would incorporate spatial and vertical variations in currents. Depending on the resulting transport, the location of spawning grounds may be better defined, leading to better protection of this valuable fishery resource. Information on recruitment variability and key environmental factors affecting larval transport are essential to accurately interpret stock assessments, maintain the ecological integrity of both spawning grounds and nursery grounds, and to effectively manage the pink shrimp fishery.

Acknowledgments

We are especially grateful to Thomas Lee and Elizabeth Williams (RSMAS, University of Miami), Elizabeth Johns, Ryan Smith, Shailer Cummings, and Nelson Melo (NOAA/AOML, Miami), and Ned Smith (Harbor Branch Oceanographic Institute) for providing ADCP data and valuable comments; to William Richards (NMFSC/NOAA Miami) and Robert Cowen (RSMAS, University of Miami) for their constructive comments and support; to Hernando Cardenas (NMFSC) for his assistance sorting plankton samples; to Andre Daniels (USGS, Miami), for his valuable support of fieldwork; and to the personnel involved in collecting and managing data from C-MAN and COMP stations. This research was funded by the NOAA South Florida Ecosystem Resto-

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ration Prediction and Modelling (SFERPM) program through a cooperative agreement between Southeast Fisheries Science Center, USGS and CIMAS, RSMAS, University of Miami, and the DOI Critical Ecosystems Studies Initiative of the Everglades Restoration Program. The sampling that supported this research was conducted pursuant to National Park Service Permit no. EVER-2003-SCI-0109 and Florida Fish and Wildlife Conservation Commission Special Activity License no. 03SR-502.

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Biology and assessment of the painted sweetlips (*Diagramma pictum* (Thunberg, 1792)) and the spangled emperor (*Lethrinus nebulosus* (Forsskål, 1775)) in the southern Arabian Gulf

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Abstract—The population biology and status of the painted sweeplips (*Diagramma pictum*) and spangled emperor (*Lethrinus nebulosus*) in the southern Arabian Gulf were established by using a combination of size-frequency, biological, and size-at-age data. Transverse sections of sagittal otoliths were characterized by alternating translucent and opaque bands that were validated as annuli. Comparisons of growth characteristics showed that there were no significant differences ($P>0.05$) between sexes. There were well defined peaks in the reproductive cycle, spawning occurred from April to May for both species, and the mean size at which females attained sexual maturity was 31.8 cm fork length (L_F) for *D. pictum* and 27.6 cm (L_F) for *L. nebulosus*. The mean sizes at first capture (21.1 cm L_F for *D. pictum* and 26.4 cm L_F for *L. nebulosus*) were smaller than the sizes for both at first sexual maturity and those at which yield per recruit would be maximized. The range of fishing-induced mortality rates for *D. pictum* (0.37–0.62/yr) was substantially greater than the target (F_{opt}=0.07/yr) and limit (F_{limit}=0.09/yr) estimates. The range of fishing-induced mortality rates for *L. nebulosus* (0.15/yr to 0.57/yr) was also in excess of biological reference points (F_{opt}=0.10/yr and F_{limit}=0.13/yr). In addition to growth overfishing, the stocks were considered to be recruitment overfished because the biomass per recruit was less than 20% of the unexploited levels for both species. The results of the study are important to fisheries management authorities in the region because they indicate that both a reduction in fishing effort and mesh-size regulations are required for the demersal trap fishery.

Manuscript submitted 29 December 2003 to the Scientific Editor's Office.
Manuscript approved for publication 11 July 2005 by the Scientific Editor.
Fish. Bull. 104:75–88 (2006).

The painted sweetlips (*Diagramma pictum* (Thunberg, 1792)), is a member of the family Haemulidae and is widely distributed throughout the Indo-West Pacific, from the Red Sea and East Africa to Japan and New Caledonia (Randall et al., 1997). Adults are found in shallow coastal waters and coral reefs down to a depth of 80 m, and juveniles are often found in weedy areas (Smith and McKay, 1986). The diet of this species consists of benthic invertebrates and fishes (Sommer et al., 1996). It is a relatively large tropical species attaining 100 cm fork length and 6 kg in total weight (Torres, 1991); consequently it is exploited throughout its range with a variety of gears, including handlines, traps, and nets (Fischer and Bianchi, 1984). *Diagramma. pictum* has a gonochoristic reproductive mode and spawning occurs annually with one clear seasonal peak (Breder and Rosen, 1966).

Fishes of the family Lethrinidae are abundant in the coastal tropical and subtropical Indo-Pacific (Young and Martin, 1982). The spangled emperor (*Lethrinus nebulosus* (Forsskål, 1775)), is distributed throughout the Indo-West Pacific from the Red Sea and East Africa to southern Japan and Samoa. It is found in a variety of habitats including coral reefs, sea grass beds and mangroves from near shore to a depth of 75 m (Randall, 1995). Adults are either solitary or are found in small schools, and juveniles form large schools in shallow, sheltered sandy areas. The diet of this species is mainly composed of mollusks, crustaceans, polychaete worms, and echinoderms (Fischer and Bianchi, 1984).

As with other representatives of the family Lethrinidae, *L. nebulosus* is a protogynous hermaphrodite, and sexual transformation from female to male occurs over a wide range of sizes (Young and Martin, 1982; Ebisawa, 1990). Lethrinids are considered to have long spawning seasons, running from spring to at least early fall, with spring and fall peaks. Spawning occurs after dark for most species in aggregations along the inner or outer edge of the fringing reef (Johannes, 1981). *Lethrinus nebulosus* is a large tropical species reaching 80.0 cm total length and 8.4 kg total weight (Randall, 1995) and is exploited throughout its range with a variety of gears (Fischer and Bianchi, 1984).

Both species form an important part of fisheries landings in the southern Arabian Gulf, where they are mainly caught with dome-shaped wire traps that have a hexagonal mesh of approximately 3.5 cm in diameter. Traps are either set individually or in strings from traditional wooden dhows, sets are made to a maximum depth of 40 m, and vessels fish an

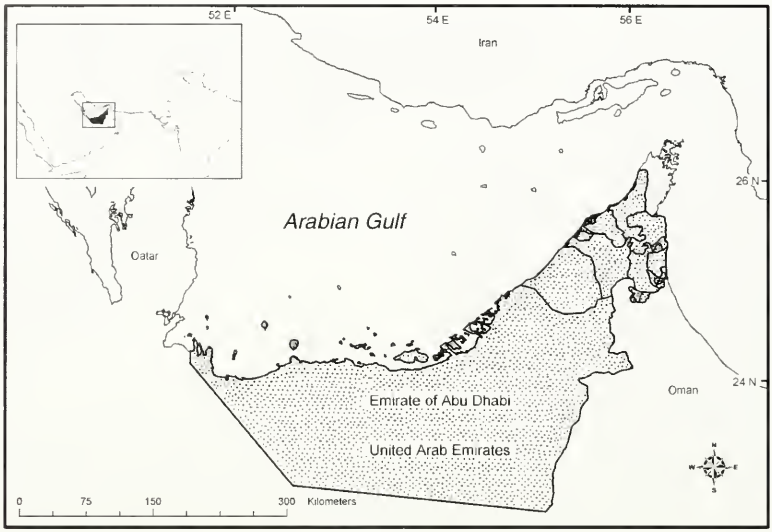

Figure 1

Study site (stippled area) showing the location of the Emirate of Abu Dhabi, off the coast of which data were collected for the painted sweetlips (*Diagramma pictum*) and spangled emperor (*Lethrinus nebulosus*) from commercial catches.

average of 210 traps each. Collection of catch-and-effort data for the fisheries of the Emirate of Abu Dhabi in the United Arab Emirates was initiated in 2001. However, many species, including *D. pictum* and *L. nebulosus*, are recorded to the family level, and therefore the use of statistical catch-at-age methods can not be used for conducting assessments at the species level. Landings of haemulids (predominantly *D. pictum*) and lethrinids (predominantly *L. nebulosus*), totaled 719 and 2911 metric tons, respectively, in the Emirate of Abu Dhabi during 2003 (Grandcourt et al.[1]). Despite the limited time scale for which catch and effort data are available, there has been an overall increase in fishing effort and catches since 2001.

Many of the fish populations in the Arabian Gulf have been heavily exploited (Samuel et al., 1987), and fishing effort may have already been above optimum levels for most demersal species (Siddeek et al., 1999). The expansion of the fishing fleet of the United Arab Emirates and the lack of appropriate data on most stocks underscore the need to assess the fisheries resources of the region. The goal of this study was to evaluate the status of *D. pictum* and *L. nebulosus* and to provide biological reference points and other pertinent information required for management. Specific objectives included establishing key demographic parameters by using validated age estimates, identifying reproductive characteristics and conducting yield-per-recruit analyses for the selected study species.

Materials and methods

Study site and sampling protocol

Size-frequency data were collected from commercial catches made off the coast of the Emirate of Abu Dhabi in the United Arab Emirates (Fig. 1) between September 2000 and March 2003. Fish were selected at random from landings and fork length (L_F) was recorded to the nearest cm by using a measuring board. Monthly target sample sizes were 500 individuals per species.

Biological data was collected from specimens purchased from commercial catches between June 2002 and May 2003. Samples were obtained from 30 individuals of each species from a representative size range during the last week of each month. Standard length (L_S), fork length (L_F), and total length (L_T) were recorded to the nearest mm by using a measuring board. Whole wet weight was measured with an electronic balance and recorded to the nearest g. The sex of a fish was determined by macroscopic examination of the gonad, which

[1] Grandcourt, E. M., F. Francis, A. Al Shamsi, K. Al Ali, and S. Al Ali. 2004. Annual fisheries statistics for Abu Dhabi Emirate 2003, 87 p. Environmental Research and Wildlife Development Agency, P.O. Box 45553, Government of Abu Dhabi, United Arab Emirates.

was removed and subsequently weighed to 0.1 g with an electronic balance.

Sagittal otoliths were extracted, cleaned in water, dried, and stored in seed envelopes. One of each pair of sagittae was weighed to 0.1 mg, burnt on a hotplate until it changed to a dark brown color, and embedded in epoxy resin. Transverse sections through the nucleus (of approximately 200–300 μm thickness) were obtained by using a twin blade saw. Sections were mounted on glass slides and examined with a low-power microscope and transmitted light.

Age and growth

The number of opaque bands in transverse sections was recorded in addition to the optical characteristics of the outer margin (opaque or translucent). The proportion of samples with opaque or translucent margins was calculated for each month and used to infer the timing and periodicity of increment formation. The age at which the first opaque band formed was calculated as the time between the mean birth date and the time of formation of opaque bands. Subsequently, the absolute age was calculated as the age at formation of the first band plus the number of opaque bands outside the first band and the time between the formation of the last band and capture. In order to establish the relationship of the timing of opaque zone formation with trends in sea water temperature, time series data were converted by using the scaling process given in Newman and Dunk (2003).

Growth was investigated by fitting the von Bertalanffy growth function (von Bertalanffy, 1938) to size-at-age data using standard nonlinear optimization methods. The model was fitted to pooled data and each sex separately. The von Bertalanffy growth function is defined as follows:

$$L_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where L_t = length at time t;
L_∞ = the asymptotic length;
k = the instantaneous growth coefficient; and
t_0 = the hypothetical time at which length is equal to 0.

Growth curves were compared between sexes for each species by using the analysis of residual sums of squares method of Chen et al. (1992).

The growth performance index Φ' (Gayanilo and Pauly, 1997) was calculated in order to provide a basis for the comparison of growth characteristics in terms of length:

$$\Phi' = \Phi - 2/3 \log_{10}(a),$$

where $\Phi = \log_{10}(k) + 0.67 \log_{10}(W_\infty)$ and $W_\infty = aL_\infty^3$.

The constant, a, was derived from length-weight relationships and k and L_∞ were obtained from the von Bertalanffy growth function.

Parameters of the length-weight relationship were obtained by fitting the power function $W = aL_F^b$ to length and weight data where W is the total wet weight, a is a constant determined empirically, L_F is the fork length, and b is close to 3.0 for species with isometric growth. Ratios of total length (L_T) to fork length (L_F) were also calculated for each species.

Reproduction

The mean size at first sexual maturity was estimated for females by fitting the logistic function to the proportion of mature fish in 2-cm (L_F) size categories. The mean size at first maturity was taken as that at which 50% of individuals were mature. Gonadosomatic indices, calculated by expressing gonad weight as a proportion of total body weight, were plotted against the sample period by month to establish the timing and seasonality of spawning. The mean birth date was estimated from patterns in reproductive indices.

Population sex ratios were examined by using χ^2 goodness-of-fit tests. Independent tests were conducted to determine whether sex ratios differed significantly from unity for whole samples and for size and age categories within samples. The probability level was set at 0.05 (α=0.05) and Yates's correction factor was used on account of there being only one degree of freedom for each comparison. Juvenile retention was calculated as the proportion of fish in aggregated size-frequency samples below the mean size at first sexual maturity.

Mortality and selectivity

Size-at-age data were used to construct age-length keys following the method of Ricker (1975) and these were used to convert aggregated length-frequency data into age-frequency distributions. The number of fish above the age at which fish were fully recruited to the fishery was calculated as a proportion of the total number of fish. The annual instantaneous rate of total mortality (Z) was subsequently determined with the age-based catch curve method (Beverton and Holt, 1957). The natural logarithm of the number of fish in each age class was plotted against the corresponding age, and Z (±95% CI) was estimated from the descending slope of the best fitting line by using least-squares linear regression. Initial ascending points representing fish that were not fully recruited to the fishery were excluded from the analyses.

The annual instantaneous rate of total mortality was also estimated with the length-converted catch method of Pauly (1983). Pooled length-frequency samples were converted into relative age-frequency distributions by using parameters of the von Bertalanffy growth function. The natural logarithm of the number of fish in each relative age group divided by the change in relative age was plotted against the relative age, and Z (±95% CI) was estimated from the descending slope of the best fitting line with least-squares linear regression. The estimates of Z from age-based and length-

converted catch curves were compared by using a modified t-test (Sokal and Rohlf, 1995).

Backwards extrapolation of the length-converted catch curves was used to estimate the probability of capture data. Selectivity curves were generated by fitting a logistic function to the plot of the probability of capture against size, from which values of the parameters L_{50}, L_{75}, and the size at which fish were fully recruited to the fishery (L_{100}) were obtained.

Estimates of the annual instantaneous rate of natural mortality (M) were obtained for each species with the empirical equation derived by Hoenig (1983). Maximum age estimates of 31 years for *D. pictum* and 21 years for *L. nebulosus* from the literature (Loubens, 1980; Edwards and Shaher, 1991) were used because the maximum ages and sizes obtained in our study were considerably lower than other reported values.

The annual instantaneous rate of fishing-induced mortality (F) was calculated by subtracting the natural mortality rate (M) from the total mortality rate (Z) derived from age-based catch curves ($F=Z-M$). The calculation was also made for the upper and lower 95% confidence intervals for estimates of Z in order to derive a range of fishing mortality rate estimates. The exploitation rate (E) was calculated as the proportion of the fishing mortality in relation to total mortality ($E=F/Z$).

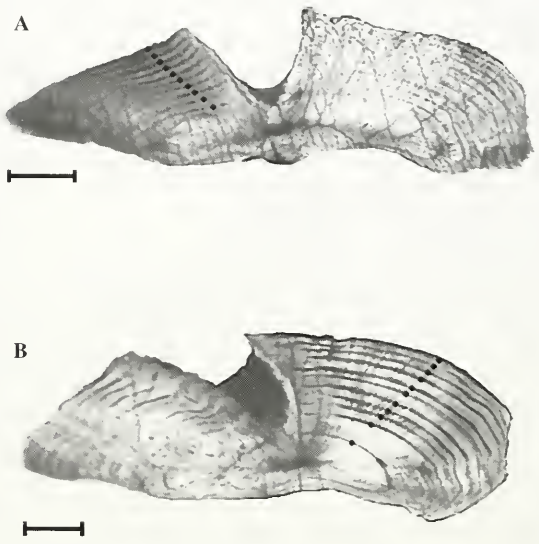

Figure 2

Photomicrographs of transverse sections through the sagittal otoliths of (**A**) *Diagramma pictum*, 56.0 cm L_F and (**B**) *Lethrinus nebulosus*, 45.7 cm L_F. Dots show opaque zones (scale bar=1 mm).

Assessment of the fishery

Relative yield and biomass-per-recruit analyses were used to assess the fishery. Growth (k and L_∞), mortality (M), and selectivity (L_{50}) parameters were used as model inputs, and knife-edge selection was assumed. The Beverton and Holt (1966) yield-per-recruit (YPR) model modified by Pauly and Soriano (1986) was used to estimate the sizes at maximum yield per recruit (L_{max}) and to predict the effects of increasing the mean size at first capture (L_{50}) to the mean size at first sexual maturity (L_{mat}) and that at which yield per recruit would be maximized (L_{max}). Estimates of exploitation rates representing 1) a marginal increase of relative yield per recruit which is 0.1 of its value at the origin ($E_{0.1}$) and 2) maximum yield (E_{max}) were also derived from the model. The exploitation rates corresponding to F_{opt} and F_{limit} (E_{opt} and E_{limit}) were calculated and used to estimate the relative biomass per recruit for each species for L_{50}, L_{mat}, and L_{max} from relative biomass-per-recruit curves. Precautionary target (F_{opt}) and limit (F_{limit}) biological reference points were calculated as 0.5 and 2/3 M, respectively, and used to infer resource status by direct comparison with the fishing mortality rates established for the study species.

Results

Age and growth

Alternating translucent and opaque growth increments were observed in transverse sections of the sagittal otoliths of *D. pictum* and *L. nebulosus* when viewed with transmitted light under low-power magnification (Fig. 2). For both species, one growth increment consisting of an opaque and translucent zone was formed on an annual basis. Opaque bands formed in the summer months between May and September in association with increasing sea water temperatures (Fig. 3); conversely translucent zones were deposited in the autumn and winter (October to February) in association with decreasing sea water temperatures.

The maximum age estimates determined from counts of opaque bands were 13 and 14 years for *D. pictum* and *L. nebulosus*, respectively. Size-at-age relationships were asymptotic in form and there was considerable individual variability in growth (Fig. 4) (parameters of the von Bertalanffy growth function are given in Table 1). A comparison of the growth characteristics between sexes revealed that there were no significant differences in parameter estimates for both species ($P=0.125$, df=319 for *D. pictum* and $P=0.878$, df =324 for *L. nebu-*

losus). Values of the growth performance index Φ' for growth in length were 2.81 for *D. pictum* and 2.80 for *L. nebulosus*.

The length-weight relationship provided a good fit to length and weight data for *D. pictum* ($W=1\times10^{-5}\times L^{2.99}$) ($r^2=0.994$) and *L. nebulosus* ($W=3\times10^{-5}\times L^{2.88}$) ($r^2=0.992$). Ratios of total length (L_T) to fork length (L_F) were 1.11:1.0 for *D. pictum* and 1.07:1 for *L. nebulosus*.

Reproduction

The mean size at first sexual maturity (L_{mat}) for *D. pictum* was 30.7 cm L_F for males (24.3–37.2 cm 95% CI) and 31.8 cm L_F for females (24.3–38.9 cm 95% CI). Those for *L. nebulosus* were 28.6 cm L_F (23.7–33.8 cm 95% CI) and 27.6 cm L_F (19.6–35.6 cm 95% CI) for males and females, respectively.

There was a peak in the gonadosomatic index for both *D. pictum* and *L. nebulosus* females in April, the main spawning period lasted until the end of May (Fig. 5), and the mean birth date was estimated as 1 May. There was a significant ($P<0.05$) female bias in the overall sex ratios (male to female) of 1:2.8 for *D. pictum* and 1:2.6 for *L. nebulosus*. The results of chi-square goodness-of-fit tests conducted for the sex ratios in both age and size categories revealed that the female bias was consistent across all categories for *L. nebulosus* although the bias was removed in the oldest age and largest size classes of *D. pictum* (Tables 2 and 3).

The proportion of fish in aggregated size-frequency samples that were below the mean size at first sexual maturity for females (juvenile retention rate) was 35.1% for *D. pictum* and 10.9% for *L. nebulosus*.

Mortality and selectivity

Modal age groups in age-frequency distributions derived from age-length keys and size-frequency data were 3 years for *D. pictum* and 5 years for *L. nebulosus* (Fig. 6). The proportion of fish above the age at which fish were fully recruited was 13.8% and 45.7% for *D. pictum* and *L. nebulosus*, respectively. There were no significant differences between the total mortality rate estimates derived from age-based and length-converted catch curves for *D. pictum* ($t=0.81$, $P=0.43$, 15 df) and *L. nebulosus* ($t=0.03$, $P=0.98$, 11 df) (Fig. 7). Fishing mortality rates were in excess of the natural mortality rates, accounting for 79% and 64% of the total mortality for *D. pictum* and *L. nebulosus*, respectively (Table 4).

The selectivity range derived from plots of the probability of capture at size was 25.0 cm for *D. pictum* (18.0–43.0 cm) and 34.0 cm for *L. nebulosus* (13.0–47.0 cm) (Fig. 8). Values of the sizes where the probability of capture was 50% (L_{50}), 75% (L_{75}), and 100% (L_{100}) are given in Table 5. For both species, fish were recruited

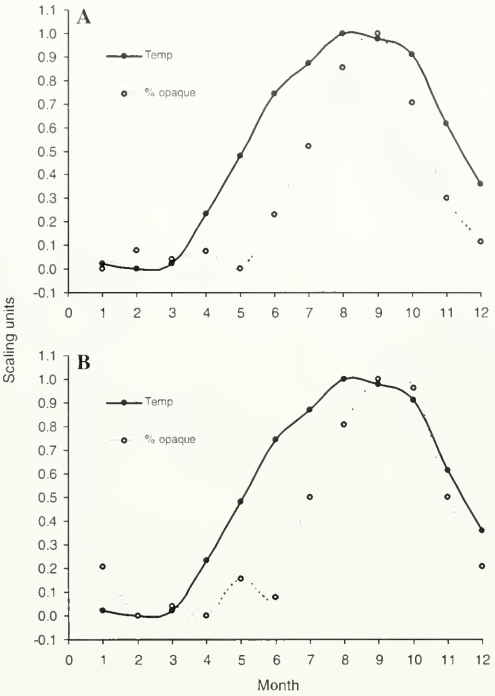

Figure 3

The proportion of otoliths with opaque outer margins for (**A**) *Diagramma pictum* ($n=348$) and (**B**) *Lethrinus. nebulosus* ($n=343$) and monthly sea temperatures off the Emirate of Abu Dhabi. Note that the values have been converted to a standardized scale to enable comparison of the trends.

Table 1

Parameters of the von Bertalanffy growth function, coefficients of determination (r^2), and sample sizes (n) for *Diagramma pictum* and *Lethrinus nebulosus* in the southern Arabian Gulf.

	D. pictum			*L. nebulosus*		
	Males	Females	All	Males	Females	All
k	0.29	0.23	0.24	0.10	0.11	0.11
L_∞ cm (L_F)	60.6	63.8	63.0	69.9	65.2	66.2
t_0 (yr)	−1.2	−1.5	−1.4	−3.3	−2.9	−3.0
r^2	0.86	0.83	0.84	0.91	0.88	0.79
n	81	244	325	86	244	330

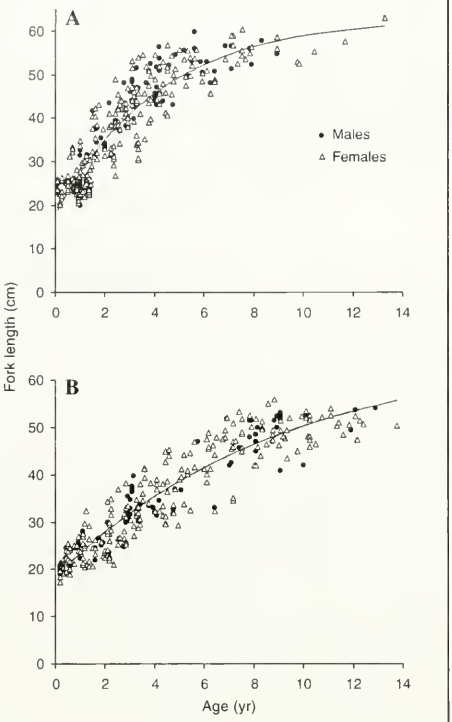

Figure 4

The von Bertalanffy growth function fitted to size-at-age relationships for (**A**) *Diagramma pictum* and (**B**) *Lethrinus nebulosus*.

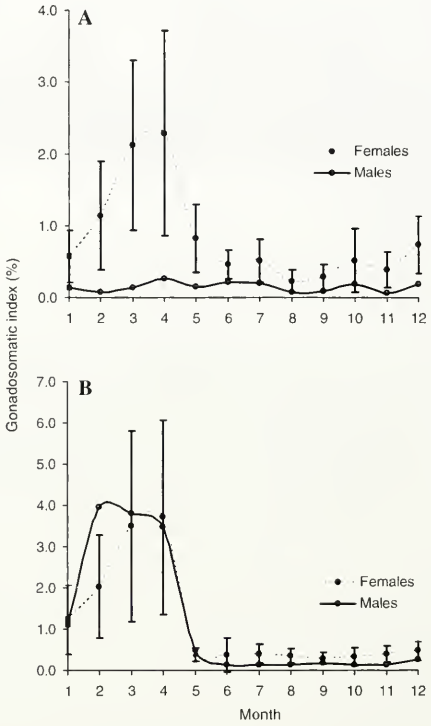

Figure 5

Mean monthly gonadosomatic indices (±SE) for (**A**) *Diagramm pictum* (n=359) and (**B**) *Lethrinus nebulosus* (n=360).

Table 2

Results of chi-square goodness-of-fit tests on sex ratios within age categories for *Diagramma pictum* and *Lethrinus nebulosus* (* significant at α=0.05).

Age category (yr)	No. of males	No. of females	Chi-square (total)	P
D. pictum				
0–2	29	130	64.2	<0.01*
3–5	38	91	21.8	<0.01*
6–13	16	29	3.8	>0.05
L. nebulosus				
0–2	34	93	27.4	<0.01*
3–6	29	88	29.8	<0.01*
7–14	27	69	18.4	<0.01*

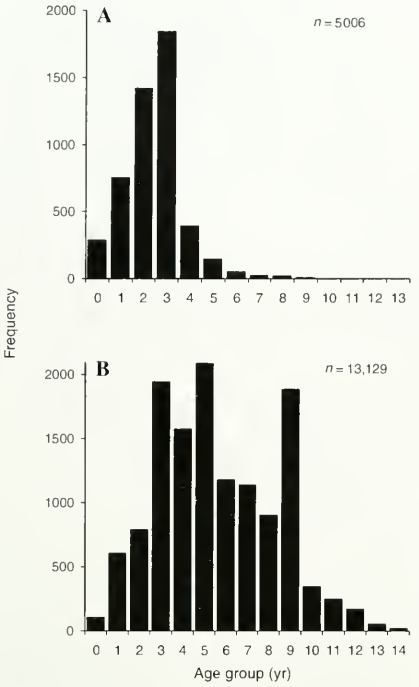

Figure 6

Age-frequency distributions for (**A**) *Diagramma pictum* and (**B**) *Lethrinus nebulosus* derived from age-length keys and size-frequency data.

to the fishery at a mean size (L_{50}) which was smaller than the mean size at which first sexual maturity was attained (L_{mat}).

Assessment of the fishery

The size at which yield per recruit would be maximized (L_{max}) was 44.4 cm (L_F) for *D. pictum* and 36.9 cm (L_F) for *L. nebulosus*. For both species, these values were considerably greater than the mean size at first capture and the mean size at first sexual maturity (Fig. 9).

The exploitation rate for *D. pictum* (0.79/yr) was greater than that which would maximize yield per recruit (0.57/yr) at the existing mean size at first capture (Table 6). Furthermore, the same yield per recruit could be achieved at a much lower exploitation rate and at an increased relative biomass per recruit (Fig. 10). The yield-per-recruit function also indicated that an increase in the size at first capture to that which would

Table 3

Results of chi-square goodness-of-fit tests on sex ratios within size categories for *Diagramma pictum* and *Lethrinus nebulosus* (*=significant at α=0.05).

Size category (cm L_F)	No. of males	No. of females	Chi-square (total)	*P*
D. pictum				
20–34	26	128	67.6	<0.01*
35–49	41	93	20.2	<0.01*
50–64	27	43	3.7	>0.05
L. nebulosus				
15–29	40	121	40.8	<0.01*
30–44	41	89	17.7	<0.01*
45–54	26	73	22.3	<0.01*

Table 4

Mortality and exploitation rates (±95 CI) for *Diagramma pictum* and *Lethrinus nebulosus*.

	D. pictum	*L. nebulosus*
Total mortality rate/yr (Z)		
(Age-based catch curve)	0.63 (0.50–0.75)	0.56 (0.35–0.77)
(Length-converted catch curve)	0.69 (0.58–0.79)	0.56 (0.53–0.60)
Natural mortality rate/yr (M)	0.13	0.20
Fishing mortality rate/yr (F)	0.50 (0.37–0.62)	0.36 (0.15–0.57)
Exploitation rate/yr (E)	0.79	0.64

Table 5

Probability of capture (selectivity) for *Diagramma pictum* and *Lethrinus nebulosus*.

Probability of capture	*D. pictum* cm (L_F)	*L. nebulosus* cm (L_F)
50% (L_{50})	21.1	26.4
75% (L_{75})	30.7	35.1
100% (L_{100})	40.3	43.8

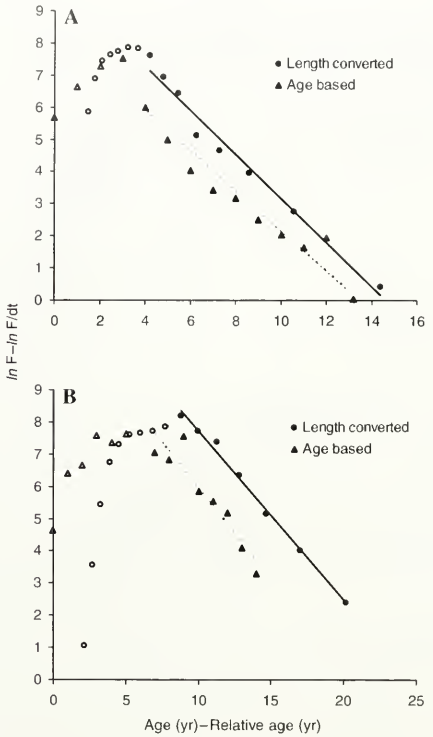

Figure 7

Age-based catch curves (ln$F$ against Age) and length-converted catch curves (ln F/dt against $Relative\ age$) for *Diagramma pictum* (**A**) and *Lethrinus nebulosus* (**B**). Dashed and solid lines show the regression equation ($y=bx+a$) fitted to data for age-based and length-converted catch curves, respectively. Only solid points are included in the regressions.

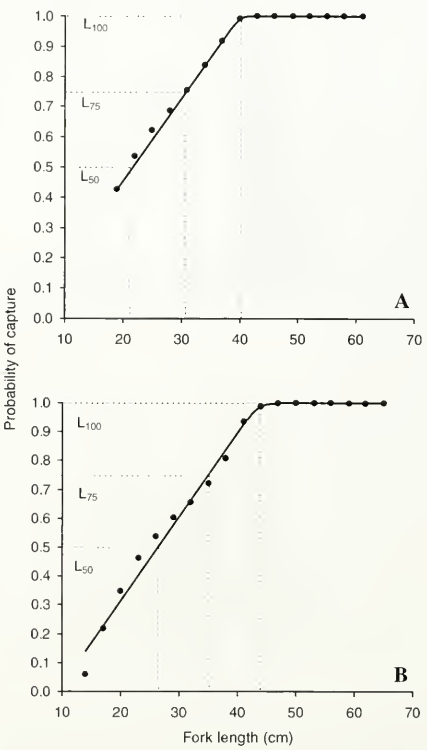

Figure 8

Selectivity curves for (**A**) *Diagramma pictum* and (**B**) *Lethrinus nebulosus*, showing the mean size at first capture at probabilities of 0.5 (L_{50}), 0.75 (L_{75}), and the size at which fish are fully recruited to the fishery (L_{100}).

Table 6

Exploitation rates ($E_{0.1}$ and E_{max}) at the existing size at first capture (L_{50}), the size at first capture at sexual maturity (L_{mat}) and the size at first capture at maximum yield per recruit (L_{max}) for *Diagramma pictum* and *Lethrinus nebulosus*.

Exploitation rate	*D. pictum*			*L. nebulosus*		
	L_{50}	L_{mat}	L_{max}	L_{50}	L_{mat}	L_{max}
$E_{0.1}$ (/yr)	0.50	0.56	0.75	0.51	0.56	0.75
E_{max} (/yr)	0.57	0.65	0.81	0.63	0.65	0.86

maximize yield per recruit would be associated with a substantial increase in yield at the current level of exploitation. An increase in the size at first capture to that at which sexual maturity occurs (L_{mat}) was also predicted to be associated with an increase in yield, although to a lesser degree (Fig. 10).

The relative biomass per recruit for *D. pictum* at the current exploitation rate was less than 10% of that at the theoretical unexploited level. An increase in the mean size at first capture to that which would maximize yield per recruit was predicted to be associated with a small increase in biomass per recruit. Changes in the exploitation rate were predicted to have a greater impact on biomass per recruit, which was estimated to be above 50% of the unexploited level at the optimum exploitation rate (E_{opt}) (Table 7).

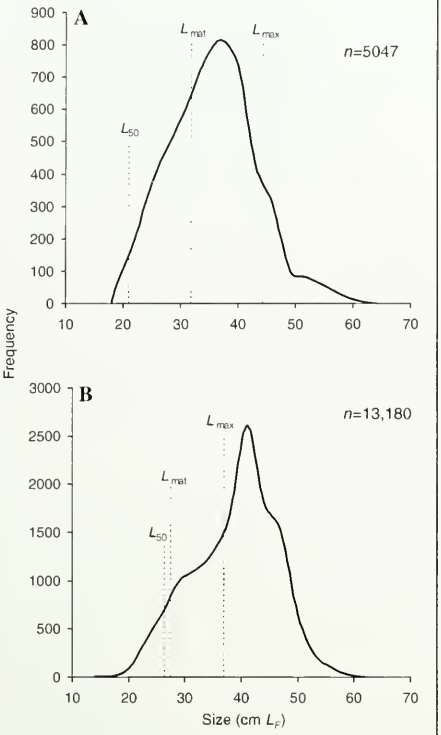

Figure 9

Aggregated length-frequency distributions for (**A**) *Diagramma pictum* and (**B**) *Lethrinus nebulosus* showing the mean sizes at first capture (L_{50}), sexual maturity (L_{mat}), and the size at first capture which would maximize yield per recruit (L_{max}).

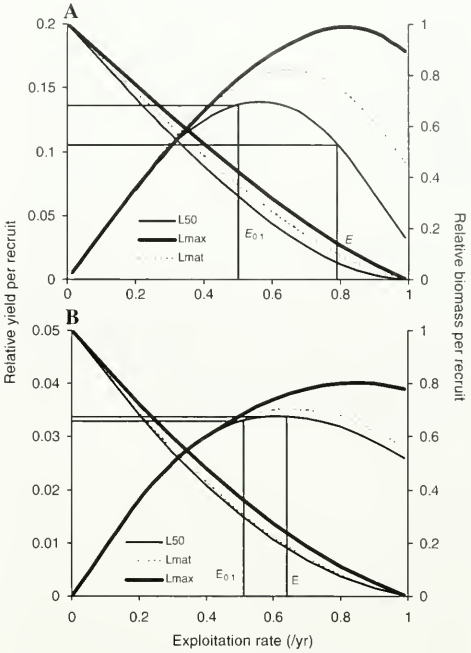

Figure 10

Relative yield and respective biomass-per-recruit curves (descending lines) for (**A**) *Diagramma pictum* and (**B**) *Lethrinus nebulosus* showing the existing exploitation rate (E) and the exploitation rate at which the slope of the yield-per-recruit curve is 0.1 of its value at the origin ($E_{0.1}$). Curves show the effect of increasing the existing mean size at first capture (L_{50}) to the mean size at first sexual maturity (L_{mat}) and the size which would maximize yield per recruit (L_{max}).

Estimates of precautionary target and limit exploitation rates (E_{opt} and E_{limit}) for *D. pictum* were 0.34 and 0.40, respectively.

The exploitation rate for *L. nebulosus* (0.64/yr) was marginally greater than that which would maximize yield per recruit (0.63/yr) at the existing mean size at first capture (Table 6). The yield-per-recruit function indicated that an increase in the size at first capture to that which would maximize yield per recruit would be associated with an increase in yield at the current level of exploitation. An increase in the size at first capture to that at which sexual maturity occurs (L_{mat}) was also predicted to be associated with an increase in yield, although to a lesser degree (Fig. 10).

The relative biomass per recruit for *L. nebulosus* at the current exploitation rate was less than 20% of that

Table 7

Relative biomass per recruit at precautionary exploitation rates (E_{opt} and E_{limit}) at the existing size at first capture (L_{50}), the size at first capture at sexual maturity (L_{mat}), and the size at first capture at maximum yield per recruit (L_{max}) for *Diagramma pictum* and *Lethrinus nebulosus*.

	Relative biomass per recruit					
	D. pictum			*L. nebulosus*		
Exploitation rate	L_{50}	L_{mat}	L_{max}	L_{50}	L_{mat}	L_{max}
E_{opt} (/yr)	0.52	0.55	0.60	0.50	0.51	0.53
E_{limit} (/yr)	0.44	0.48	0.53	0.39	0.40	0.45

at the theoretical unexploited level. An increase in the mean size at first capture to that which would maximize yield per recruit was predicted to be associated with a small increase in biomass per recruit. Changes in the exploitation rate were predicted to have a greater impact on biomass per recruit, which was estimated to be above 50% of the unexploited levels at the optimum exploitation rate (E_{opt}) (Table 7). Estimates of precautionary target and limit exploitation rates (E_{opt} and E_{limit}) for *L. nebulosus* were 0.33 and 0.43, respectively. For both *D. Pictum* and *L. nebulosus*, the exploitation rates predicted from the yield per recruit function ($E_{0.1}$ and E_{max}) were equal to or in excess of values where $F=M$ (0.5) for all sizes at first capture.

The range of fishing mortality rates estimated for *D. pictum* (0.37–0.62/yr) was substantially greater than both the target (F_{opt}=0.07/yr) and limit (F_{limit}=0.09/yr) biological reference points. The range of fishing mortality rates for *L. nebulosus* (0.15/yr to 0.57/yr) were also in excess of the biological reference points for this species (F_{opt}=0.10/yr and F_{limit}=0.13/yr).

Discussion

Age and growth

The formation of alternating translucent and opaque growth zones in fish otoliths has been associated with a variety of factors, including seasonal variations in water temperature, photoperiod, feeding, and reproduction (Moe, 1969; Reay, 1972; Panella, 1980; Manickchand-Heileman and Phillip, 2000). Although the mechanisms of growth-increment formation are poorly understood, the deposition of the opaque zone in tropical species generally occurs in the spring and summer months during periods of accelerated growth, whereas the translucent zone is formed when there is reduced metabolic activity (Beckman and Wilson, 1995). The formation of opaque and translucent zones in the sagittal otoliths of *D. pictum* and *L. nebulosus* determined in our study follows this generalized pattern.

The southern Arabian Gulf exhibits marked seasonal variability in oceanographic characteristics; sea water temperatures can exceed 34°C in summer and fall to 21°C in the winter (Sheppard et al., 1992). The close association of the formation of opaque zones with increasing seawater temperature indicates that temperature could be the principal environmental signal stimulating the deposition of these growth zones. Other allied variables, such as productivity and subsequent food availability, may also be associated with seasonal growth-rate oscillations and the formation of growth increments. The validation of the annual periodicity of increment formation adds to a growing body of evidence (Fowler, 1995) and dismisses the misconception that annuli do not form in the otoliths of reef fish due to a lack of seasonality in the tropics (e.g., Sparre and Venema, 1992). Nevertheless, the edge analysis method used should ideally be conducted over a 2-year cycle and could have been more rigorous with the use of larger sample sizes and by conducting the analyses for individual ages. Furthermore, it is important to distinguish between the validation of increment periodicity and absolute age (Campana, 2001). Although our study has provided empirical evidence for an annual pattern of increment formation, the absolute age of the study species remains to be validated. Validation of the absolute age could be achieved through independent means such as a mark-recapture study and the chemical marking of juvenile fish of known age.

The maximum number of opaque bands counted for *D. pictum* in the present study (13) was considerably less than the maximum age of 31 years estimated by Loubens (1980) for this species in New Caledonia. Likewise, our longevity estimate of 14 years for *L. nebulosus* was less than that of Mathews and Samuel (1991) (20 years) and of Edwards and Shaher (1991) (21 years) for this species in the northern Arabian Gulf and Gulf of Aden, respectively. Our longevity estimates therefore were most likely to have been underestimated owing to the absence of fish close to the maximum reported sizes for these species.

A method of validating growth parameters involves the comparison of growth performance indices (Φ') in terms of growth in length with other estimates obtained for the same or a similar species (Gayanilo and Pauly, 1997). Values of Φ' for *D. pictum* available from other studies have ranged from 2.88 (Loubens, 1980) to 3.24 (Baillon and Kulbicki, 1988), and an estimate of 3.07 has been obtained for this species in the Gulf of Aden (Edwards et al., 1985). The estimate obtained in our study (2.81) compares with the lower end of this range. Values of Φ' for *L. nebulosus* have ranged from 2.55 (Kuo and Lee, 1986) to 3.41 (Baillon, 1991), and an estimate of 2.87 obtained for this species in the northern Arabian Gulf in the waters off Kuwait (Baddar, 1987) compares well with our estimate of 2.80. Although the growth parameters in our study would appear to be of the right order (by comparison), improvements in our estimates could have been made by the addition of larger specimens close to the maximum size for both species.

Despite its widespread use, the von Bertalanffy growth function may not be suitable for hermaphroditic populations (Appeldoorn, 1996). Growth analyses have shown distinct differences in the sizes of equal-age males and females of protogynous species (Moe, 1969; Nagelkerken, 1979; Garratt et al., 1993), and experiments have shown what are considered to be growth accelerations leading to sex change (Ross et al., 1983). Failure to account for growth spurts in yield models can result in significant over estimation of both maximum yield and optimal effort (Bannerot et al., 1987). Although *L. nebulosus* is a protogynous hermaphrodite (Young and Martin, 1982; Ebisawa, 1990), the results of the analysis of residual sums of squares in our study indicated that there are no differences in the growth characteristics between sexes and that the use of growth parameters from pooled data would therefore be justified in yield-per-recruit analyses.

Reproduction

Simulation models and evidence of the effects of fishing have shown that protogynous species are far more vulnerable to fishing pressure than comparable gonochoristic stocks (Huntsman and Schaaf, 1994). For protogynous species, in which males tend to be larger than females on average, there are indications that size-selective fishing mortality may result in the differential loss of larger males (Sadovy, 1996) and the possibility that insufficient males remain in the reproductive population to fertilize eggs from all females (Koenig et al., 1996). In this context, *L. nebulosus* may be particularly vulnerable to such effects because the female-biased sex ratios were consistent throughout all the age categories and size classes. The overall female bias and removal of the bias in the oldest and largest age category for *D. pictum* is generally representative of the sexual structure of a protogynous population. Given these characteristics, histological confirmation of the reproductive mode of this species should be considered.

The well-defined spawning period of *D. pictum* and *L. nebulosus* between April and May supports the view that seasonal reproductive cycles are common among tropical fishes (Robertson, 1990; Montgomery and Galzin, 1993; Sadovy, 1996). There were high levels of juvenile retention for *D. pictum* (35.1%) because fish were recruited to the fishery before the mean size at which sexual maturity occurred, indicating a need to increase the mesh size of traps.

Mortality and selectivity

Estimates of natural mortality derived from other studies of *D. pictum* range from 0.43/yr (Edwards et al., 1985) to 0.67/yr (Baillon and Kulbicki, 1988). The comparatively low value of M obtained in our study (0.13/yr) can be attributed to the difference in methods used, but errors in other estimates from the empirically derived formula of Pauly (1980) may have occurred because the relationship has tended to overestimate M, especially for slow growing species (e.g., Ralston, 1987; Russ et al., 1998). Similarly, our value of the instantaneous natural mortality rate for *L. nebulosus* (0.20/yr) was lower than other estimates that range from 0.279/yr (Edwards et al., 1985) to 1.18/yr (Baillon, 1991). Although estimates of M derived from the Hoenig (1983) relationship have been shown to provide a reasonable approximation of M in tropical demersal fishes (Hart and Russ, 1996; Newman et al., 1996), errors in this parameter were potentially the greatest source of error in our assessment.

Upward bias in estimates of the total mortality rate (Z) may have occurred if larger fish were less vulnerable to the fishing gear or if adult fish underwent migrations, for example. A survey of the biomass of demersal species in the Arabian Gulf waters of the United Arab Emirates showed that there were no seasonal changes in the abundance of *L. nebulosus* and the haemulid *Plectorhinchus sordidus* (Shallard[2]). This finding indicates that ontogenetic or spawning-associated migrations would unlikely be altering the size and age composition and subsequent estimates of Z for the species investigated. Although size-specific selectivity cannot be discarded as a possible explanation for the small proportion of larger and older fish in size-frequency and biological samples, the impact of fishing on the size and age structure of the respective populations is considered a more likely reason for these observations and is likely to be the probable cause given the historic absence of regulation in the trap fishery.

Because the size at first capture (21.1 cm L_F) was considerably smaller than the size at which yield per recruit would be maximized (44.4 cm L_F) for *D. pictum*, an increase in the mesh size for the trap fishery should be considered by management authorities especially given the high rate of juvenile retention for this species. The same is applicable for *L. nebulosus* with a mean size at first capture of 26.4 cm L_F and size at maximum yield per recruit of 36.9 cm L_F.

Assessment of the fishery

The use of yield-per-recruit models may be particularly restrictive for fast growing tropical species with high rates of natural mortality because the curves may not reach a maximum within a reasonable range of fishing mortality values (Gayanilo and Pauly, 1997). Although the species examined in our study were relatively slow growing and had low rates of natural mortality, failure of the yield-per-recruit model may still have occurred at the upper end of the fishing mortality range.

Gulland (1970) suggested that in an optimally exploited stock, fishing mortality should be about equal to natural mortality, resulting in an exploitation rate of 0.5/yr. However, exploitation rates should be very conservative for relatively long-lived reef fish (Newman and Dunk, 2003), especially given that potential yields may be over estimated by a factor of 3–4 where $F=M$ (Beddington and Cooke, 1983). With a range from 0.5 to 0.86/yr, the exploitation rates derived from yield-per-recruit analyses ($E_{0.1}$ and E_{max}) are considered to have overestimated the associated fishing mortality rates.

The relative yield-per-recruit analyses indicated that an increase in the size at first capture of *D. pictum* and *L. nebulosus* to that which would maximize yield per recruit would be associated with increases in yields at the existing exploitation rates. However, the existing exploitation rate for *D. pictum* (0.79/yr) was greater than that which would maximize yield per recruit (E_{max}=0.57/yr). Although the exploitation rate for *L. nebulosus* (0.64/yr) was comparable to that which would maximize yield per

[2] Shallard, B. 2003. Distribution and abundance of demersal fish stocks in the UAE, 211 p. Technical Report 1. Fish Resources Assessment Survey Project of Abu Dhabi and UAE Waters. Bruce Shallard and Associates and Environmental Research and Wildlife Development Agency, P.O. Box 45553, Government of Abu Dhabi, United Arab Emirates.

recruit (0.63/yr), given that E_{max} was probably overestimated, the results indicate that growth overfishing is also occurring for this species.

The specified precautionary target (F_{opt}=0.5.M) and limit (F_{limit}=2/3.M) values are considered to be more appropriate biological reference points in light of the constraints of the yield-per-recruit model. The range of fishing mortality rates estimated for *D. pictum* (0.37–0.62/yr) was substantially greater than both the target (F_{opt}=0.07/yr) and limit (F_{limit}=0.09/yr) biological reference points, and the existing exploitation rate (0.79/yr) was more than double the optimum level (0.34/yr). The range of fishing mortality rates for *L. nebulosus* (0.15/yr to 0.57/yr) were also in excess of the biological reference points for this species (F_{opt}=0.10/yr and F_{limit}=0.13/yr) and the exploitation rate (0.64/yr) was approximately double the optimum target level (0.33/yr). This result clearly indicates growth overfishing for both species and, in combination with the results of the yield-per-recruit analyses, demonstrates that effort reductions are also required in the fishery because target reference points cannot be achieved by modification of the gear-selectivity characteristics alone.

A critical limitation of the yield-per-recruit model is the assumption that there is no relationship between the size of the spawning stock biomass and recruitment (Buxton, 1992). Even if the size at first capture is less than the size at first sexual maturity, the stock size may approach zero at high levels of fishing mortality in spite of predictions of high levels of yield per recruit. It is therefore important to consider the size of the spawning stock biomass across the range of fishing mortality rates when interpreting results. The relative biomass per recruit of *D. pictum* and *L. nebulosus* at the estimated fishing mortality rates was particularly low at less than 10% and 20%, respectively, of unexploited levels. If the critical spawning stock biomass is between 20% and 50% of the unexploited levels, as suggested by King (1995), recruitment overfishing is likely to be occurring for both species. This is most clearly seen in the age structure for *D. pictum*, for which only 13.8% of the total number of fish were above the age at which fish were fully exploited by the gear (ages 4–13 years). For this species, the majority of the yield was derived from the newly recruited age class representing fish that had just become fully vulnerable to the gear.

The relative biomass per recruit at the exploitation rates that were equivalent to F_{opt} corresponded to 52% and 51% of the theoretical unexploited biomass levels for *D. pictum* and *L. nebulosus*, respectively. The associated levels of fishing mortality are therefore considered appropriate target reference points, given the present fisheries policy which is aimed at resource conservation and stock rebuilding. Accordingly, the results of our study are important to fisheries management authorities in the region because they indicate that both a substantial reduction in fishing effort and an increase in mesh-size of traps are currently necessary for the previously unregulated demersal trap fishery.

Acknowledgments

We are very grateful to Sultan Al Ali, Khaled Al Ali, John Hoolihan, and Kunath Gopalan for their assistance with data collection and Abdulla Aboubaker for helping with data entry. Howard Choat and Will Robbins assisted in the training of technicians in otolith processing. The comments of the anonymous reviewer helped considerably in improving the manuscript. This study was funded by the Government of the United Arab Emirates through the Environmental Research and Wildlife Development Agency's Marine Environment Research Centre.

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A catch-free stock assessment model with application to goliath grouper (*Epinephelus itajara*) off southern Florida

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Abstract—Many modern stock assessment methods provide the machinery for determining the status of a stock in relation to certain reference points and for estimating how quickly a stock can be rebuilt. However, these methods typically require catch data, which are not always available. We introduce a model-based framework for estimating reference points, stock status, and recovery times in situations where catch data and other measures of absolute abundance are unavailable. The specific estimator developed is essentially an age-structured production model recast in terms relative to pre-exploitation levels. A Bayesian estimation scheme is adopted to allow the incorporation of pertinent auxiliary information such as might be obtained from meta-analyses of similar stocks or anecdotal observations. The approach is applied to the population of goliath grouper (*Epinephelus itajara*) off southern Florida, for which there are three indices of relative abundance but no reliable catch data. The results confirm anecdotal accounts of a marked decline in abundance during the 1980s followed by a substantial increase after the harvest of goliath grouper was banned in 1990. The ban appears to have reduced fishing pressure to between 10% and 50% of the levels observed during the 1980s. Nevertheless, the predicted fishing mortality rate under the ban appears to remain substantial, perhaps owing to illegal harvest and depth-related release mortality. As a result, the base model predicts that there is less than a 40% chance that the spawning biomass will recover to a level that would produce a 50% spawning potential ratio.

Manuscript submitted 30 April 2004 to the Scientific Editor's Office.
Manuscript approved for publication 14 July 2005 by the Scientific Editor.
Fish. Bull. 104:89–101 (2006).

The last decade has witnessed considerable interest in the so-called precautionary approach to resource management, where human activities are curtailed to prevent further environmental degradation without the burden of proving that these activities are to blame. Fisheries applications of the precautionary approach typically hinge on the notion that fishing pressure should be reduced in a predetermined fashion as certain "limit" reference points are approached (FAO, 1995; Caddy, 1998; Restrepo et al., 1998). In the United States, the Magnuson-Stevens Fishery Conservation and Management Act (Public Law 94-265) mandates the development of fishery management plans (FMPs) that specify criteria for determining when a stock is overfished and the remedial measures necessary to ensure a timely recovery. The National Standard Guidelines developed by the National Marine Fisheries Service to implement the Act require each FMP to include an "MSY control rule" that comprises two reference points, known as the maximum fishing mortality threshold (MFMT) and the minimum stock size threshold (MSST). When the abundance of the stock dips below the MSST, special provisions must be made to rebuild the stock to the level that would support the maximum sustainable yield within a time frame that is as short as possible and that is commensurate with the intrinsic productivity of the stock and the needs of the fishing community.

Many modern stock assessment methods provide the machinery for determining limit reference points as well as for appraising where the stock is in relation to them and how quickly it can be rebuilt. However, these methods typically require data on total catch or absolute abundance, which are not always available. In the case of goliath grouper (*Epinephelus itajara*), for example, a recent review panel concluded that the catch statistics were unreliable and not useful for assessment purposes (Anon.[1]). Several *ad hoc* control rules have been developed to accommodate such "data-poor" situations. One of the more common is simply to define the MSST in terms of historical indices of abundance that supposedly represent a desirable stock condition (Annala, 1993; Cadrin et al., 2004). An advantage of this type of approach is that it is model-free, and nothing is assumed concerning the recovery rate of the stock. Being model-free, however, is a disadvantage with respect to the requirements of the Magnuson-Stevens Act, inasmuch as the recovery time cannot be estimated. Moreover, there may be other types of information that could influence the perception of the status of the stock, and it would be useful to integrate that information formally into the assessment.

[1] Anon. 2003. Goliath grouper data workshop report. SEDAR3-DW-1, 11 p. South Atlantic fishery Management Council, 1 Southpark Circle, Charleston SC 29406.

The purpose of this article is to introduce a model-based framework for estimating reference points, stock status, and recovery times in situations where catch data and other measures of absolute abundance are unreliable. The specific estimator developed in this study is essentially an age-structured production model recast in terms relative to pre-exploitation levels. A Bayesian estimation scheme is adopted to allow the incorporation of pertinent auxiliary information such as might be obtained from meta-analyses of similar stocks or anecdotal observations. The approach is applied to the population of goliath grouper off southern Florida, which is believed to have been severely depleted during the 1980s and has been protected from all harvest since 1990 (GMFMC[2]).

Materials and methods

Population dynamics model

The study period begins when the stock is believed to be near virgin levels, such that the relative abundance N of each age class a at the beginning of the first year is given by

$$N_{a,1} = \begin{cases} 1 & a = a_r \\ N_{a-1,1} e^{-M_{a-1}} & a_r < a < A \\ N_{A-1,1} e^{-M_{A-1}} / (1 - e^{-M_A}), & a = A \end{cases} \quad (1)$$

where a_r = the youngest age class in the analysis;
A = a "plus-group" representing age classes A and older; and
M = the natural mortality rate.

The relative abundance at the beginning of subsequent years (y) is modeled by the recursion

$$N_{a,y} = \begin{cases} r_y & a = a_r \\ N_{a-1,y-1} e^{-F_{y-1} v_{a-1} - M_{a-1}} & a_r < a < A \\ N_{A-1,y-1} e^{-F_{y-1} v_{a-1} - M_{a-1}} + & \\ N_{A,y-1} e^{-F_{y-1} v_A - M_A}, & a = A \end{cases} \quad (2)$$

where r_y = the annual recruitment to age class a_r relative to virgin levels;
F = the fishing mortality rate on the most vulnerable age class; and
v_a = the relative vulnerability of the remaining age classes (which implicitly includes factors such as gear selectivity, size limit regulations, and the fraction of the stock exposed to the fishery).

Relative recruitment (r) is modeled as a first-order lognormal autoregressive process,

$$r_y = \mu_r e^{\varepsilon_y}$$
$$\varepsilon_y = \rho_r \varepsilon_{y-1} + \eta_{r,y}, \quad (3)$$

where μ_r = the median expectation
ρ_r = the correlation coefficient; and
η = normal-distributed random variates having mean 0 and standard deviation σ_r (ostensibly representing the effect on recruitment of fluctuations in the environment).

The median is modeled by the Ricker or Beverton-Holt spawner-recruit functions recast in terms of the maximum lifetime reproductive rate α and relative spawning biomass s:

$$\mu_r = \begin{cases} s_{y-a_r} \alpha^{1 - s_{y-a_r}} & \text{Ricker} \\ \dfrac{\alpha s_{y-a_r}}{1 + (\alpha - 1) s_{y-a_r}} & \text{Beverton and Holt} \end{cases} \quad (4)$$

$$s_y = \sum_{a=a_r}^{A} E_a e^{-(F_y v_a + M_a) t_s} N_{a,y} / \sum_{a=a_r}^{A} E_a e^{-M_a t_s} N_{a-1},$$

where E = an index of the per-capita number of eggs produced by each age class (E); and
t_s = the fraction of the year elapsed at the time of spawning.

The shapes of these two curves are essentially the same as the conventional relationships (Fig. 1); however their domain is implicitly limited to the interval $0 \le s \le 1$ (see Appendix 1 for a derivation).

The fishing mortality rate on the most vulnerable age class F is also modeled as a first-order lognormal autoregressive process,

$$F_y = \mu_F e^{\delta_y}$$
$$\delta_y = \rho_F \delta_{y-1} + \eta_{F,y}, \quad (5)$$

where μ_F = the median level;
ρ_F = the correlation coefficient; and
η = normal-distributed random variates having mean 0 and standard deviation σ_F.

The median annual is generally assumed to be proportional to an index of fishing effort f:

$$\mu_F = \phi f_y, \quad (6)$$

[2] GMFMC (Gulf of Mexico Fishery Management Council). 1990. Amendment number 2 to the fishery management Plan for the reef fish fishery of the Gulf of Mexico, 31 p. Gulf of Mexico Fishery Management Council. 3018 North US Highway 301, Suite 1000, Tampa, FL 33619.

where ϕ can vary among three eras of exploitation: a "prehistoric" period, during which little data are available; a "modern" period, when presumably there are some data on abundance or mortality rates; and a "future" period, when fishing mortality rates are controlled (input). The absence of data during the "prehistoric era" generally precludes the estimation of annual deviations in recruitment (ε) or fishing mortality rate (δ) during that period.

The average weight or fecundity of the plus group is expressed as a function of the average age of the plus-group. Initially, it is assumed that the age composition of the plus-group is in equilibrium consistent with Equation 1, in which case the average age of the plus-group at the beginning of the first year is approximately

$$\bar{a}_{A,1} = A + \frac{e^{-M_A}}{1-e^{-M_A}}. \tag{7}$$

Subsequently, the age of the plus-group is updated as

$$\bar{a}_{A,y+1} = \frac{AN_{A-1,y}e^{-F_y v_{A-1} - M_{A-1}} + (\bar{a}_{A,y}+1)N_{A,y}e^{-F_y v_A - M_A}}{N_{A,y+1}}. \tag{8}$$

Reference points

Equations 1–4 describe the relative dynamics of a population apart from its absolute abundance. As such they are suitable for developing management plans where the fishing mortality rate is controlled directly (e.g., by reducing effort) and the biomass reference points are expressed on a relative scale. When the virgin spawning biomass itself is used as the reference point, the estimated value of s_y is a direct measure of the status of the stock. For example, if the management goal is to maintain spawning biomass at or above 50% of the virgin level, then estimates of s below 0.5 may trigger some action to reduce fishing pressure.

A related reference point is the equilibrium spawning potential ratio (Goodyear, 1993), defined as the expected lifetime fecundity per recruit at a given F (ψ_F) divided by the expected lifetime fecundity in the absence of fishing (ψ_0):

$$p = \frac{\psi_F}{\psi_0}, \qquad \psi_F = \sum_{a=0}^{A} E_a e^{-(F v_a + M_a)\gamma_s} e^{-\sum_{i=0}^{a-1} F v_i + M_i}. \tag{9}$$

As shown in Appendix 2, the corresponding equilibrium level of relative spawning biomass (denoted by a tilde) may be computed as

$$\tilde{s}_p = \begin{cases} 1 + \dfrac{\log_e p}{\log_e \alpha} & \text{Ricker} \\ \dfrac{\alpha p - 1}{\alpha - 1} & \text{Beverton and Holt} \end{cases} \tag{10}$$

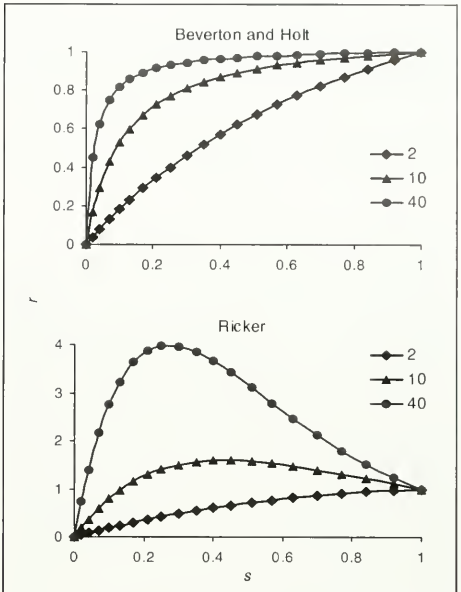

Figure 1

Examples of scaled Beverton-Holt and Ricker spawner-recruit relationships for various values of α (maximum lifetime fecundity). The labels s and r refer to relative spawning biomass and relative recruitment, respectively.

Note that $\tilde{s}_p$ is independent of the vulnerability vector v. Accordingly, MSST definitions based on $\tilde{s}_p$ will have the desirable property of being insensitive to changes in fishery behavior.

Other management plans employ reference points such as F_{max} or $F_{0.1}$, which are based on the yield per recruit statistic

$$\left(\frac{Y}{R}\right) = \sum_{a=0}^{A} w_a F v_a \frac{1-e^{-(F v_a + M_a)}}{F v_a + M_a} e^{-\sum_{i=0}^{a-1} F v_i + M_i}, \tag{11}$$

where w_a is some measure related to the average weight of the catch. Inasmuch as there are no terms involving the absolute abundance of the stock, the calculation of such statistics poses no special problems for the relative framework presented in the present study. Prescriptions based on the maximum sustainable yield (MSY) are slightly more complicated because equilibrium yield is the product of equilibrium recruitment $\tilde{R}$ and equilibrium yield per recruit:

$$\tilde{Y} = \tilde{R}_F \sum_{a=0}^{A} w_a F v_a \frac{1-e^{-(F v_a + M_a)}}{F v_a + M_a} e^{-\sum_{i=0}^{a-1} F v_i + M_i}. \tag{12}$$

However, the fishing mortality rate that maximizes Equation 12 also maximizes Equation 12 divided by the virgin recruitment R_0 (a constant). Thus, F_{MSY} may be obtained from

$$\max_F \left\{ \frac{F\tilde{s}_p}{p} \sum_{a=0}^{A} w_a v_a \frac{1-e^{-(Fv_a+M_a)}}{Fv_a+M_a} e^{-\sum_{i=0}^{a-1} Fv_i+M_i} \right\}. \quad (13)$$

where $\tilde{s}_p/p$ has been substituted for $\tilde{R}_F/R_0$.

The values of p and $\tilde{s}_p$ corresponding to F_{max} , $F_{0.1}$, or F_{msy} may be calculated by means of Equations 9 and 10, respectively. Note however, that p is no longer the target value specified by management, but a derivative of the targeted values of F. This means that MSST definitions based on $\tilde{s}_{max}$, $\tilde{s}_{0.1}$, and $\tilde{s}_{msy}$ will vary somewhat with the behavior of the fishery. In some cases this could lead to risk prone situations where the perception of stock status changes simply because the fishery targets different age groups (i.e., the definition of MSST changes rather than the abundance of the resource). In the case of MSY, a more stable alternative is to define the MSST in terms of a "spawn at least once" policy where mature animals are regarded as fully vulnerable to the fishery and immature animals area regarded as invulnerable.

Parameter estimation

The equations above include numerous "unknowns" representing the processes of reproduction, mortality, and growth. In the case of "data-poor" stocks like goliath grouper, there are insufficient data to estimate all of these unknown parameters with an acceptable level of precision. However, it is often possible to increase the precision of the estimates through the use of Bayesian prior probability densities constructed to reflect expert opinion (e.g., Wolfson et al., 1996; Punt and Walker, 1998) or based on meta-analyses involving similar species (e.g., Liermann and Hilborn, 1997; Maunder and Deriso, 2003).

The Bayesian approach to estimation seeks to develop a "posterior" probability density for the parameters Θ that is conditioned on the data D, $P(\Theta \mid D)$. By application of Bayes rule it is easy to show that

$$P(\Theta \mid D) \propto P(D \mid \Theta) P(\Theta). \quad (14)$$

where $P(D \mid \Theta)$ is the sampling density (likelihood function); and $P(\Theta)$ is the prior density (in this case the analyst's best guess of the probability density for Θ).

Estimates for Θ may be obtained by integrating the posterior (the classical Bayes moment estimator; cf. Gelman et al., 1995)

$$\bar{\theta}_j = \int \theta_j P(D \mid \Theta) P(\Theta) d\theta_j, \qquad \theta_j \in \Theta \quad (15)$$

or by minimizing its negative logarithm (the highest posterior density estimator; Bard, 1974)

$$\min_{\Theta} \left\{ -\log_e P(D \mid \Theta) - \log_e P(\Theta) \right\}. \quad (16)$$

In the present model, a prior needs to be specified for the parameters reflecting recruitment (α and ε_y), mortality (M, ϕ, δ_y, v_a), fecundity (E_a), and growth in weight (w_a). It is assumed in the present study that the parameters are statistically independent with respect to prior knowledge, such that the joint prior is merely the product of the marginal priors for each parameter. The exceptions are the process error functions for the annual recruitment and fishing mortality rate deviations, ε_y and δ_y. These are assumed to be autocorrelated lognormal variates with negative- log density functions of the form

$$-\log P(\varepsilon) = \frac{1}{2\sigma_r^2} \left[\varepsilon_1^2 + \sum_y (\varepsilon_{y+1} - \rho_r \varepsilon_y)^2 \right] + \log \sigma_r, \quad (17)$$

where ρ_r = the correlation coefficient; and
σ_r^2 = the variance of $\log_e \eta_r$.

For stability reasons, it is assumed that $\varepsilon_0 = 0$.

It is possible, at least in principle, to conduct an assessment based on prior specifications alone. However, it may be difficult to develop sufficiently informative priors for some of the parameters, particularly for the fishing mortality rates. The preferred approach, of course, is to condition the estimates on data. With the present model it is assumed that catch data are either unavailable or unreliable, otherwise a standard age-structured production model (cf. Restrepo and Legault, 1998) would be more appropriate. However, time series of catch-per-unit-of-effort data or fishery-independent surveys are often available even when total catches are not. To the extent that changes in these data (c) are proportional to changes in the abundance of the population as a whole (N), they may be modeled as

$$\begin{aligned} c_{i,y} &= q_i \sum_a v_{i,a} N_{a,y} e^{-(F_y v_a + M_a) t_i} e^{\gamma_{i,y}} \\ \gamma_{i,y} &\sim Normal(0, \sigma_{c,i}), \end{aligned} \quad (18)$$

where i indexes the particular survey time series;
q = the proportionality coefficient scaling the time series to the relative abundance of the population;
t_i = the fraction of the year elapsed at the time of the survey;
$\sigma_{c,i}$ = the standard deviation of the fluctuations in $\log_e c_i$ owing to observation errors or changes in the distribution of the stock; and
v_a and $v_{i,a}$ = the relative vulnerability of each age class to the fishery and the i^{th} survey, respectively.

The corresponding negative logarithm of the sampling density is

$$-\log P(c\,|\,\Theta) = \sum_{i}\sum_{y}\left\{\frac{1}{2\sigma^2_{c,i}}\left(\log_e(c_{i,y}) - \log_e\left(q_i\sum_a v_{i,a}N_{a,y}e^{-(F_y v_{i,a}+M_a)t_i}\right)\right)^2 + \log\sigma_{c,i}\right\}. \quad (19)$$

Anecdotal observations may be treated in similar fashion. For example the perceptions of constituents on the abundance of the resource relative to virgin levels (n) can be modeled as

$$n_y = \frac{\sum_a \lambda_a N_{a,y} e^{-(F_y v_{i,a}+M_a)\Delta}}{\sum_a \lambda_a e^{-M_a\Delta} e^{-\sum_{i=0}^{a-1} M_i}} e^{\gamma_{n,y}} \quad (20)$$

$$\gamma_{n,y} \sim Normal(0,\sigma_n).$$

Here λ_a is the relative contribution of each age class in forming the perception of total abundance (e.g., fishermen may never encounter very young fish), Δ is the time of the year most reflective of the period upon which the perceptions were based (e.g., the peak of the fishing season), and σ_n is the standard deviation of the fluctuations in $\log_e n_y$.

It is not generally possible to obtain consistent estimates for all of the elements of the covariance matrix **V** (i.e., ρ_F, σ^2_F, ρ_r, σ^2_r, $\sigma^2_{c,i}$ and σ^2_n). In the case of survey data, the variances associated with sampling variability are often estimated extraneous to the population model (e.g., during the standardization procedure). However, there may be additional variance owing to fluctuations in the distribution of the stock in relation to the survey area (IWC, 1994). To accommodate such possibilities, the survey variance parameters are modeled as

$$\sigma^2_{c,i,y} = \chi^2_{c,i,y} + \beta_{c,i}\sigma^2$$
$$\sigma^2_{n,y} = \chi^2_{n,y} + \beta_n\sigma^2, \quad (21)$$

where the $\chi^2_{c,i,y}$ and $\chi^2_{n,y}$ = the annual observation variances (estimated outside the model);

σ^2 reflects some overall process variance (estimated within the model); and

β = constant multipliers (usually fixed by the analyst based on a careful consideration of the inherent variability of the underlying processes).

The recruitment variance and correlation coefficient are generally inestimable without a good index of recruitment and may have to be fixed to some moderate values (say σ_r=0.4 and ρ=0.5).

Table 1

Anecdotal reports from nine individuals concerning the abundance of adult-size goliath grouper (*Epinephelus itajara*) in 1990 in relation to their abundance in the 1950s (expressed as percent reduction).

Interviewee	Method	% reduction
1	diver	60
2	angler	70
3	diver	75
4	angler	90
5	diver	90
6	diver	95
7	diver	95
8	diver	97
9	diver	98

The model outlined above was implemented by using the nonlinear optimization package AD Model Builder (version 4.5, Otter Research Ltd., Sidney, Canada), which provides facilities for estimating the mode and shape of the posterior distribution. Confidence intervals for the probability of recovery were generated directly from the posteriors approximated by the likelihood profile method (the accuracy of which was checked by replicating the prior distributions without data and by comparing the modes of the posterior with the HPD estimates). For some quantities confidence limits were computed by using normal approximations centered at the HPD estimate with variances obtained by inverting the Hessian matrix. This approach reduced computing time considerably, but the approximations were poor for confidence intervals broader than 80 percent owing to the thick tails and skewed nature of the posterior distributions.

Application to goliath grouper

Goliath grouper are large, long-lived predators found predominantly in the tropical western Atlantic and Caribbean Sea. They are among the least wary of reef fishes, easily approached by spearfishers and readily caught in traps or by hook and line gear. Not surprisingly, they have declined considerably throughout much of their range (Sadovy and Eklund, 1999). Although there are few data on the historic abundance of these animals in southern Florida, anecdotal reports suggest that they were much more abundant during the 1950s and 60s than they are now (Table 1). Concerns of overfishing prompted regulators in the U.S. to impose a moratorium on the harvest of goliath grouper that has remained in effect since 1990. To date, the duration of the moratorium has not been specified owing to the paucity of information on their potential recovery rates.

Spawner-recruit relationship There does not appear to be any reliable information on the nature of the

spawner-recruit relationship for any grouper species. A Beverton and Holt model was assumed in this study because it is difficult to envision a mechanism for the strong density dependence in mortality rates required by the Ricker model. A prior for the value of α (Fig. 2) was constructed from a subset of the values collected by Myers et al. (1999) that corresponds to larger, highly fecund fishes with long life spans (the 'periodic' strategists of Rose et al., 2001).

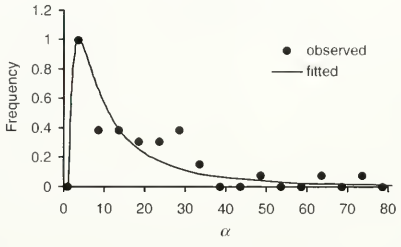

Figure 2

Lognormal prior for the maximum lifetime fecundity parameter (α) derived from the values in Myers et al. (1999) that correspond to species categorized as periodic strategists by Rose et al. (2001). The lognormal density was fitted to the values of α–1 (with median 9.8 and log-scale variance 1.31) and then was shifted 1 unit to provide a prior for α.

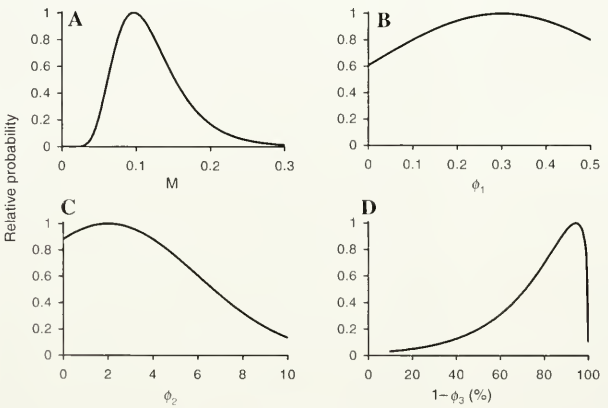

Figure 3

Priors for the mortality rate parameters: (**A**) lognormal prior for natural mortality rate, (**B**) truncated normal prior for proportionality factor ϕ_1, (**C**) truncated normal prior for multiplier ϕ_2 (**D**) gamma prior for percent reduction in F associated with the 1990 harvest ban. The upper and lower boundaries for each parameter are as given on the horizontal axes.

Fecundity and growth To date there are insufficient data for estimating a fecundity-at-age relationship for goliath grouper. We followed Legault and Eklund[3] and substituted the weight at age relationship:

$$E_a = \begin{cases} 0 & a < 6 \\ w_a = 1.31\times10^{-5} l^{3.056} & a \geq 6 \end{cases} \qquad (22)$$
$$l = 200.6\left(1 - e^{-0.126(a+0.49)}\right)$$

where w = weight in kg; and
l = length in cm expressed as a von Bertalanffy function of age (see Bullock et al., 1992).

Natural mortality The maximum observed age of 37 years (Sadovy and Eklund, 1999) suggests a value for M of about 0.11/yr according to the method of Hoenig (1983). Legault and Eklund[5] suggested a plausible range of 0.037 yr to 0.19/yr (midpoint 0.11) based on an analysis of the fraction surviving to various maximum ages. To reflect this uncertainty, a lognormal prior with a median of 0.11 and CV of 0.4 was used (Fig. 3A).

Fishing mortality rate and relative vulnerability A large fraction of the recreational landings of goliath grouper appear to come from the Ten Thousand Islands area in Southwest Florida, where most of the animals caught have been between the ages of one and five years. However, large animals were often targeted by commercial and recreational fishermen in other areas. Accordingly, we assumed the vulnerability of goliath grouper generally increased with age according to the sigmoid-shaped logistic curve

$$v_a = \frac{1}{1+e^{-(a-a_{50})/d}}. \qquad (23)$$

Estimates for the parameters a_{50} and d were obtained by fitting the curve (weighted by cumulative mortality at age) to the relative frequency of ages in two different data sets. The first data set included mostly juveniles animals between the ages of 0 and 5, obtained during creel censuses of recreational catches in the Ten Thousand Islands area of the Everglades National Park (see Porch et

[3] Legault, C. M., and A.-M. Eklund. 1998. Generation times for Nassau grouper and jewfish with comments on M/K ratios. Sustainable Fisheries Division Contribution SFD-97/98-10A, 5 p. Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.

al.[4]). The second data set included mostly adult animals obtained opportunistically from recreational and commercial catches in the eastern Gulf of Mexico (Bullock et al., 1992). The SEDAR stock assessment review panel based their advice on models that used the former selection curve (Kingsley[5]); however the effect of using the latter curve was examined as a sensitivity analysis. The two curves are contrasted in Fig. 4A.

The fishing mortality rate on the most vulnerable age class was modeled as follows:

$$F_y = \begin{cases} \phi_1 f_y & 1900 \le y \le 1979 \\ \delta_y \phi_2 F_{1979}, & 1980 \le y < 1990 \\ \phi_3 \bar{F}_{1980-89} & 1990 \le y \end{cases} \quad (24)$$

where f_y = a time series of historical effort; and
ϕ_1, ϕ_2, ϕ_3, δ_y are parameters to be estimated.

In the present study, effort was assumed to track the U.S. Census[6] for the number of people living in South Florida coastal counties between 1900 and 1980. From 1980 to 1989 this assumption was no longer required owing to the availability of several time series of relative abundance (see below). Instead, interannual variations in fishing mortality were modeled according to Equation 5 with median $\phi_2 F_{1979}$, log-scale variance $\sigma_F^2 = 0.15$ and correlation coefficient $\rho_F = 0.5$, which essentially amounts to a mild constraint on year-to-year changes in F. The nonzero correlation coefficient is intended to reflect the momentum in effective fishing effort from one year to the next that arises from a combination of market demands and the tendency of many fishermen to target only the species they are most adept at catching. Even so, the relatively large variance term admits substantial interannual variations if the data warrant them. Moreover, runs with $\rho_F = 0.0$ (no year-to-year momentum) did not produce substantially different results.

The effect of the harvest moratorium was modeled as a percentage ϕ_3 of the average fishing mortality rate in the 1980–89 period. Relatively uninformative priors were used for ϕ_1 and ϕ_2 (Fig. 3, B and C). A somewhat more informative prior with bounds between 0.01 and 0.5 was used for ϕ_3, based on the opinions of members of the SEDAR panel (Fig. 3D).

Survey information Porch and Eklund (2004) have developed relative indices of abundance from two visual surveys: the personal observations of a professional spearfisher (DeMaria[7]) and a volunteer fish-monitoring program administered by the Reef Education and Environmental Foundation (REEF 2000). In addition, Cass-Calay and Schmidt[8] have standardized catch rate data collected in the Ten Thousand Islands area by the Everglades National Park (ENP). The two visual surveys are assumed to reflect the abundance of mature fish ages 6 and older (based on diver reports of size). The ENP catch rate index, on the other hand, is assumed to reflect the relative abundance of juveniles with relative vulnerabilities given by the dome-shaped gamma function (normalized to a maximum of 1):

$$v_{ENP,a} = \left(\frac{a}{a_{100\%}} e^{1-a/a_{100\%}} \right)^{CV^{-2}-1}, \quad (25)$$

where $a_{100\%}$ = the most vulnerable age; and
CV = the coefficient of variation.

Estimates for $a_{100\%}$ (3.47) and CV (0.34) were obtained by fitting the mortality-weighted gamma curve to the frequency of ages 0 –7 in the Ten Thousand Islands data mentioned earlier (for more detail see Porch et al.[4]). The resulting curve is shown in Figure 4B.

Anecdotal impressions of stock status Johannes et al. (2000) pointed out that local fishermen often disagree with the conclusions drawn by scientists in data-poor situations and suggest that many times additional data will prove the fishermen correct. As mentioned earlier, expert judgements about the relative abundance of a stock can be treated as data or represented by a "prior." We collected information on the value of s at the time moratoriums began (1990) by interviewing fishermen and divers who had been active in southern Florida since the early 1960s or before. Specifically, interviewees were asked to state their perception of the percent reduction in goliath grouper populations from the time they began diving to the time the moratorium on catch was imposed (1990). The average percent reduction reported for large goliath (approximately age 6 and older) was 86% (standard deviation of about 13%, Table 1). This information was modeled as data in accordance with Equation 20.

[4] Porch, C. E., A-M. Eklund and G. P. Scott. 2003. An assessment of rebuilding times for goliath grouper. Sustainable Fisheries Division Contribution SFD-2003-0018. Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149. 26 p.

[5] Kingsley, M. C. S., ed. 2004. The Goliath Grouper in southern Florida: assessment review and advisory report. Report prepared for the South Atlantic Fishery Management Council, the Gulf of Mexico Fishery Management Council, and the National Marine Fisheries Service, 17 p. South Atlantic fishery Management Council, 1 Southpark Circle, Charleston SC 29406.

[6] Population of Florida Counties by Decennial Census: 1900 to 1990, 4 p. 1995. Compiled and edited by Richard L. Forstall. Population Division, U.S. Bureau of the Census. Washington, DC 20233

[7] DeMaria, D. 2004. Personal. observ. P.O. Box 420975, Summerland Key, FL 33042.

[8] Cass-Calay, S. L., and T. W. Schmidt. In review. Standardized catch rates of juvenile goliath grouper, *Epinephelus itajara*, from the Everglades National Park Creel Survey, 1973–1999.

Results

The model was able to fit the ENP index of juvenile goliath grouper very well but could not reconcile the conflicting trends indicated by the DeMaria and REEF indices for adult goliath grouper (Fig. 5). The estimated trends in spawning biomass were rather uncertain (Fig. 6A), but nevertheless indicated a rapid decline to about 5% of virgin levels by the time the harvest ban was imposed in 1990, followed by a significant increase. The estimates of fishing mortality were also somewhat uncertain, but generally indicated a gradual increase in fishing mortality to moderate levels during the 1970s followed by a rapid increase during the 1980s (Fig. 6B). The harvest moratorium was estimated to have been about 83% effective in reducing fishing mortality, nevertheless losses owing to human activities (e.g., illegal harvest and release mortality of animals caught at depth) were still estimated to be substantial (F =0.05/yr). If, in accordance with the Gulf of Mexico Management Council's generic Sustainable Fisheries Act amendment, the limit reference point is taken to be the equilibrium spawning biomass corresponding to a spawning potential ratio of 50%, then the model indicates that current fishing mortality rates are near $F_{50\%}$ and that there is less than a 50% chance the stock will recover within 15 years (Fig. 7).

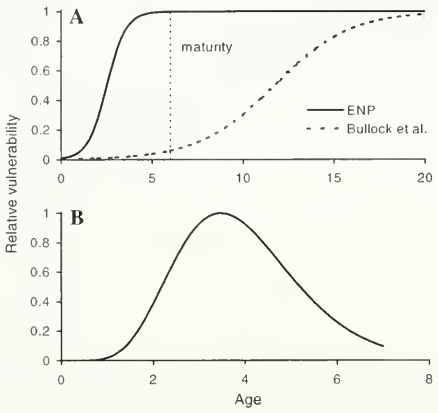

Figure 4

Selection curves used to represent the vulnerability of goliath grouper (*Epinephelus itajara*) to (**A**) the overall fishery and (**B**) Everglades National Park anglers. The logistic curves shown in (A) were fitted to either age-composition data derived from the Everglades National Park (ENP) creel census or opportunistic samples from offshore fishing trips (Bullock et al., 1992).

Sensitivity runs were conducted to examine the implications of 1) dropping one or more of the indices, 2) increasing the assumed minimum age represented in the REEF and DeMaria indices from 6 to 10, 3) assuming that the historical period began in 1950 rather than 1900 and using the anecdotal information as a tuning index and (4) using the alternate fishery selection curve that was fitted to the data from Bullock et al. (1992), where adult animals were much more vulnerable to the fishery than were juveniles. Of these, the results were most sensitive to removal of the DeMaria index—the projected trends being much more optimistic (Fig. 8). This is because the DeMaria index indicates that the adult population increased rapidly during the first few years of the harvest ban, but then suffered a set back in 1999 and has since leveled off. In contrast, the REEF index indicates that the population continued to increase during that time. Thus, when the DeMaria index is removed, the model allows for a faster postmoratorium increase in the adult population by estimating a low fishing mortality rate of about 0.01/yr (i.e., a harvest ban that is 97% effective). The fishing mortality rate estimates for the 1980s are also lower without the DeMaria index inasmuch as the DeMaria index indicates a more precipitous decline during that time than the ENP index (the REEF index does not begin until 1994).

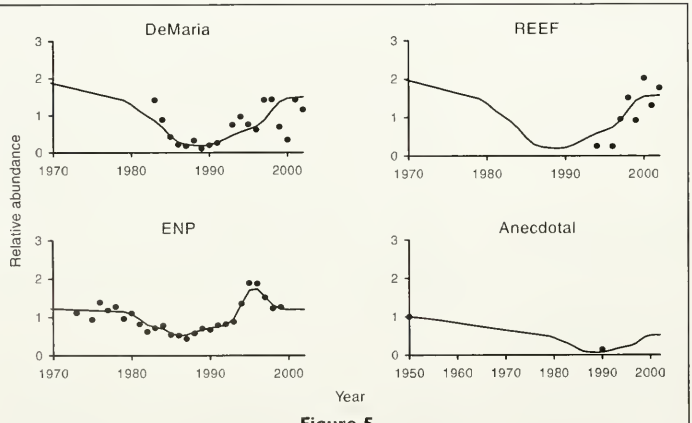

Figure 5

Base model fitted to the four indices of abundance for goliath grouper (*Epinephelus itajara*) in southern Florida.

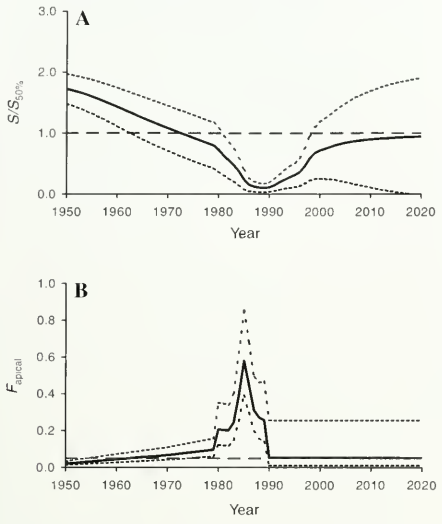

Figure 6

Base model predictions of (**A**) spawning biomass of goliath grouper (*E. itajara*) in southern Florida in relation to the equilibrium level associated with a spawning potential ratio of 50%, $s/s_{50\%}$, and (**B**) the apical fishing mortality rate on goliath grouper (*E. itajara*), F_{apical}. The lines with small dashes represent approximate 80% confidence limits and the dashed horizontal lines represent the levels associated with an SPR of 50%.

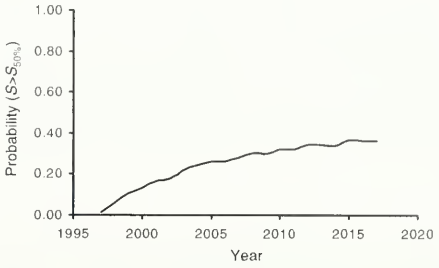

Figure 7

Predicted probability that the stock of goliath grouper (*E. itajara*) in southern Florida will have recovered to levels exceeding the equilibrium spawning biomass associated with a spawning potential ratio of 50%.

The sensitivity run with the alternate selection curve also produced more optimistic results (Fig. 8). Inasmuch as the model now attributes most of the fishing mortality to age classes well beyond the age at first maturity (see Fig. 4), the spawning stock biomass is estimated to have been reduced to a lesser extent (to about 10% of virgin levels by 1990 as compared to 5%). Thus, other things being equal, recovery requires less time. The level of $F_{50\%}$ increased with the alternate selection curve because fewer age classes are affected by fishing.

Discussion

All of the model formulations examined depicted the same qualitative patterns: escalating fishing mortality rates and rapidly declining spawning biomass, particularly during the 1980s, followed by a sharp decrease in fishing mortality and strong recovery in spawning biomass after the 1990 harvest ban. These trends are remarkably consistent with the anecdotal observations shown in Table 1 and Figure 5 as well as with the expert testimony given during the SEDAR stock assessment review. The estimated rapid increase in fishing mortality during the 1980s appears to reflect a real increase in effort that occurred due to elevated demand and selling prices (Sadovy and Eklund, 1999), as well as the widespread use of the LORAN-C navigational system (which made it easier for fishermen to relocate productive offshore shipwrecks). Thus, it seems safe to conclude that the population was overfished at the time the harvest ban was imposed and is currently undergoing a substantial recovery. Less clear is the extent to which the population has recovered since the harvest ban.

Using the base model, we estimated that the harvest ban has reduced fishing pressure by more than 50%, but probably less than 90% (Fig. 9). Thus, there is a strong chance that the current fishing mortality rate, although greatly reduced as compared to the 1980s, remains greater than $F_{50\%}$ (i.e., above 0.05/yr). This in turn translates into less than a 40% chance that the population will recover to levels above $s_{50\%}$ within the next 15 years. Several fishermen have testified that the harvest ban is probably less than 90% effective because goliath grouper are still taken illegally in places and because animals caught and released in deeper water often do not survive[7]; therefore this result does not appear unrealistic.

More optimistic results, implying a 70% to 80% chance of recovery within 15 years, were obtained when the DeMaria index was excluded or when selection was oriented more towards older animals. There does not appear to be a strong *a priori* case for excluding the DeMaria index in favor of the REEF and ENP indices. Although the coverage is rather limited, the trends of the DeMaria index are consistent with those of the ENP index (with a suitable time lag) and with anecdotal accounts of the trends in other areas.[7] The issue of selection is more vexing. It can be argued that the age-composition data from the ENP creel census adequately reflects the composition of the juvenile catch inasmuch

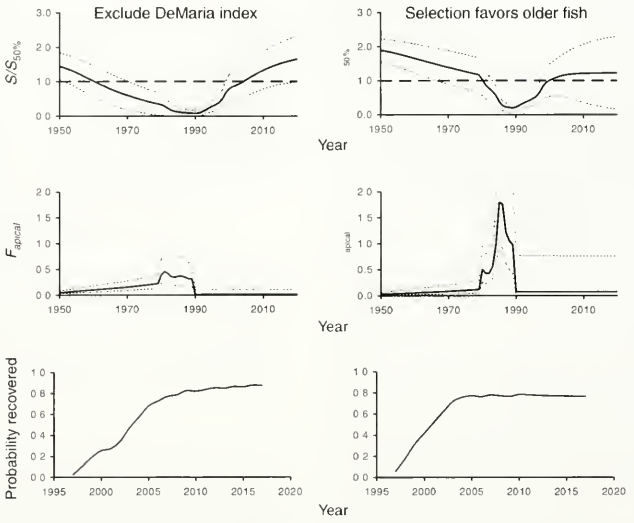

Figure 8

Trends in relative spawning biomass ($s/s_{50\%}$), apical fishing mortality rate (F), and the probability of recovery ($s>s_{50\%}$) for two sensitivity runs—one excluding the DeMaria index (left) and the other with the selection curve favoring older fish (right).

as it comes from the center of juvenile abundance; however most adults were caught outside this area of abundance. Thus, the relative contribution of juveniles and adults to the overall catch is unclear and the directional bias in the fitted logistic selection curve is uncertain.

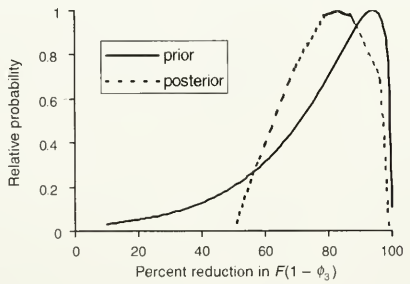

Figure 9

Posterior and prior distributions for the effectiveness of the 1990 harvest ban in reducing the fishing mortality rate F on southern Florida goliath grouper (*E. itajara*) populations (in relation to the fishing mortality rate levels observed during the 1980s).

The only other age composition information that has come to light comes from the study by Bullock et al (1992), which was not designed to provide a random sample of the catch and is probably biased towards larger animals caught on offshore wrecks. In principle, one could reflect this uncertainty more formally either by developing a prior for the selectivity parameters or else by weighting the results from the two selection models. The scientists on the SEDAR stock assessment review panel based their advice on the selection curve derived from the ENP data,[7] which is equivalent to placing negligible weight on the curve derived from the Bullock et al. (1992) data; however they recognized the selection curve as an important source of uncertainty that is difficult to address without adequate data.

It is important to emphasize that the Bayesian approach adopted in the present study allows one to explicitly model the uncertainty about parameters such as M, for which no data may exist, but a prior distribution covering the plausible range of values may be specified. There is, of course, the potential for introducing bias when one or more of the priors are based on expert opinion or otherwise subjective information. However, the same sorts of bias can be introduced by conducting sensitivity analyses where the unknown parameters are fixed to various values selected by the analysts. Furthermore, if unbiased data are in short supply, analyses

based on completely uninformative priors will be useless for generating advice because the range of plausible outcomes is too large. Accordingly, we view the use of subjective priors primarily as a vehicle for providing more realistic limits on uncertainty and prefer to express the model outcomes in terms of probability statements. For example, the point estimate from the base model indicated that the population would never recover to $s_{50\%}$ because the fishing mortality rate under the harvest ban was still slightly above $F_{50\%}$. However, consideration of the uncertainty led to the conclusion that the chance of recovering to $s_{50\%}$ within 15 years was nearly 40%.

Some sources of uncertainty have not been adequately accounted for in the above assessment. For example, the relationship between fecundity and age is unknown. We used weight-at-age as a proxy for the relative fecundity-at-age in our analysis, but it is often the case that fecundity increases with age faster than weight. If this is true for goliath grouper, then our projections would be too optimistic. It should also be remembered that the results apply strictly to the goliath grouper population in southern Florida. It is believed that the center of abundance for the population in U.S. waters is off southern Florida, particularly in the Ten Thousand Islands area, but goliath grouper are known to have occurred throughout the coastal waters of Gulf of Mexico and along the east coast of Florida, and on up through the Carolinas. Inasmuch as goliath grouper are not highly migratory, it is possible it may take some additional time for the species to fully occupy its historical range, thus delaying the overall recovery of the U.S. population.

The primary advantage of the catch-free assessment model proposed in the present study is that it does not require knowledge of the total number of removals. In this light it is worth noting that 623 of the 905 stocks included in the 2000 annual report to Congress on the Status of Fisheries were listed as having unknown status, often because catch data were either unavailable or deemed unreliable. Thus we expect the proposed method will become increasingly useful as fishery scientists are asked more and more to develop FMPs for poorly monitored fisheries. The fact that the model estimates the population's relative abundance, rather than its absolute abundance, is of little consequence when, as is often the case, adjustments to the target fishing mortality rate or catch quota are made in relation to the levels in previous years (Caddy, 2004). Moreover, certain biases tend to cancel out when dimensionless quantities like relative abundance are used. If, for example, only a consistent fraction of the population were sampled, then the absolute estimates of abundance would be biased but the relative estimates would not (Prager et al., 2003).

The greatest drawback of the catch-free method is probably its inability to provide direct estimates of the equilibrium catch levels associated with particular reference points (e.g., MSY). This situation could perhaps be ameliorated by obtaining estimates of absolute abundance from a comprehensive short-term survey covering the entire range of the animal, in which case the relative outputs from the model (including relative catch) could be appropriately scaled. Alternatively, a long-term monitoring program at select sites located throughout the known range of the animal could be established to detect changes in relative abundance under various closely monitored trial levels of catch.

Acknowledgments

The present paper benefitted greatly from the scrutiny given to a related document[6] by members of the SEDAR stock assessment review panel (R. Allen, L. Barbieri, J. Brodziak, M. Cufone, D. DeMaria, M. Kingsley, D. Murie, M. Murphy, J. Neer, J. Rooker, R. Taylor, E. Toomer, and J. Wheeler). S. Turner, L. Brooks, and two anonymous reviewers also gave helpful comments on the manuscript. S. Cass-Calay and T. Schmidt secured the goliath grouper length-composition data from the Everglades National Park creel survey; J. Brusher and J. Schull provided the age-length data from their sampling program in the Ten Thousand Islands area.

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Appendix 1: reparameterized spawner-recruit relationships

The number of young fish recruiting to a population (R) is often related to the aggregate fecundity of the spawning stock (S) by using one of two functional forms:

$$R = \begin{cases} aSe^{-bS} & \text{Ricker} \\ \dfrac{abS}{b+S}. & \text{Beverton and Holt} \end{cases} \quad \text{(A.1)}$$

The parameter a is the slope of the curve at the origin and the parameter b controls the degree of density dependence. Notice that the domain of both functions extends from zero to infinity, whereas in practice there must be some limitation on S and R even in the absence of fishing owing to environmental constraints (call them S_0 and R_0, respectively). This being so, we obtain

$$a\frac{S_0}{R_0} = \begin{cases} e^{bS_0} & \text{Ricker} \\ 1+S_0/b. & \text{Beverton and Holt} \end{cases} \quad \text{(A.2)}$$

The ratio S_0/R_0 represents the maximum expected lifetime fecundity of each recruit and a represents the survival of recruits in the absence of density dependence. Accordingly, the product $\alpha = aS_0/R_0$ may be interpreted as the maximum possible number of recruits produced by each spawner over its lifetime (Myers et al., 1999).

The dimensionless character of α makes it useful for interspecies comparisons, or for borrowing values from species with similar life history strategies. Solving for b in terms of α one obtains

$$b = \begin{cases} \log_e \alpha / S_0 & \text{Ricker} \\ S_0/(1-\alpha). & \text{Beverton and Holt} \end{cases} \quad \text{(A.3)}$$

Substituting Equation A.3 into Equation A.1 gives

$$R = \begin{cases} aS\alpha^{-S/S_0} & \text{Ricker} \\ \dfrac{aS_0}{1+(\alpha-1)S/S_0} & \text{Beverton and Holt} \end{cases} \quad \text{(A.4)}$$

and, since $a = \alpha R_0/S_0$,

$$R = \begin{cases} R_0 \dfrac{S}{S_0} \alpha^{1-S/S_0} & \text{Ricker} \\ R_0 \dfrac{\alpha S / S_0}{1+(\alpha-1)S/S_0}. & \text{Beverton and Holt} \end{cases} \quad \text{(A.5)}$$

Dividing through by R_0 and defining s as S/S_0 gives Equation 4.

Appendix 2: formula for equilibrium spawning biomass

The spawning potential ratio (p) is defined as the number of spawners produced by each recruit at equilibrium with a given fishing mortality rate F divided by the number of spawners per recruit under virgin conditions ($F=0$). This may be written

$$p = \frac{\psi_F}{\psi_0} = \frac{\tilde{S}_F / \tilde{R}_F}{\tilde{S}_0 / \tilde{R}_0} = \frac{\tilde{S}_F / S_0}{\tilde{R}_F / \tilde{R}_0} = \tilde{s} / \tilde{r}, \quad \text{(A.6)}$$

where the tilde signifies equilibrium values.

At equilibrium we also obtain from Equation 4

$$\tilde{r} = \begin{cases} \tilde{s}\alpha^{1-\tilde{s}} & \text{Ricker} \\ \dfrac{\alpha\tilde{s}}{(1+\tilde{s}(\alpha-1))}. & \text{Beverton and Holt} \end{cases} \quad \text{(A.7)}$$

Dividing both sides of Equation A.7 by $\tilde{r}$, substituting p for Equation A.6, and solving for $\tilde{s}$ gives Equation 10.

Fish assemblages found in tidal-creek and seagrass habitats in the Suwannee River estuary

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Abstract—Fish assemblages were investigated in tidal-creek and seagrass habitats in the Suwannee River estuary, Florida. A total of 91,571 fish representing 43 families were collected in monthly seine samples from January 1997 to December 1999. Tidal creeks supported greater densities of fish (3.89 fish/m^2; 83% of total) than did seagrass habitats (0.93 fish/m^2). We identified three distinct fish assemblages in each habitat: winter–spring, summer, and fall. Pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), and syngnathids characterized seagrass assemblages, whereas spot (*Leiostomus xanthurus*), bay anchovy (*Anchoa mitchilli*), silversides (*Menidia* spp.), mojarras (*Eucinostomus* spp.), and fundulids characterized tidal-creek habitats. Important recreational and commercial species such as striped mullet (*Mugil cephalus*) and red drum (*Sciaenops ocellatus*) were found primarily in tidal creeks and were among the top 13 taxa in the fish assemblages found in the tidal-creek habitats. Tidal-creek and seagrass habitats in the Suwannee River estuary were found to support diverse fish assemblages. Seasonal patterns in occurrence, which were found to be associated with recruitment of early-life-history stages, were observed for many of the fish species.

Manuscript submitted 20 July 2004 to the Scientific Editor's Office.

Manuscript approved for publication 19 July 2005 by the Scientific Editor.

Fish. Bull. 104:102–117 (2006).

The Suwannee River estuary, located on the gulf coast of Florida, is relatively pristine and supports commercial and recreational fisheries. It is an unusual estuary, with an orientation along the open coastal shoreline, and its habitats include oyster bars, mudflats, seagrasses, tidal creeks, and an extensive salt marsh (Comp and Seaman, 1985). In other estuaries of the United States, fish assemblages, species abundance, and habitat associations within estuaries have been studied extensively. Particular attention has focused on estuaries as nursery habitats for young-of-the-year (YOY) fishes that use seagrasses, tidal-creeks, and marshes during their early-life stages (Shenker and Dean, 1979; Bozeman and Dean, 1980; Livingston, 1984; Cowan and Birdsong, 1985; Gilmore, 1988; McGovern and Wenner, 1990; Baltz et al., 1993; Peterson and Turner, 1994; Rooker et al., 1998). In addition, comparisons between different habitats within estuarine systems have been conducted to evaluate the value of each habitat as a nursery (Weinstein and Brooks, 1983; Sogard and Able, 1991; Rozas and Minello, 1998; Paperno et al., 2001). Aside from basic species-composition studies of marsh fishes (Kilby, 1955; Nordlie, 2000) and fishes that inhabit shallow waters near Cedar Key (Reid, 1954), only one recent study (Tsou and Matheson, 2002) has investigated the distribution patterns of fishes in the Suwannee River estuary. Tsou and Matheson (2002) found that the nekton community structure for the Suwannee River estuary had a strong seasonal pattern that was consistent among years and followed patterns for water temperature and river discharge. They found assemblages that were associated with warm and cold seasons, and wet and dry seasons, but they did not examine habitat specific assemblages (Tsou and Matheson, 2002). For proper management of fishery resources, it is beneficial to have detailed, current information concerning the status of all life-history stages and associated habitats of species that reside in the area, as well as information concerning species interactions and associated food webs. Although human development in the Suwannee River estuary is not a current threat, the potential withdrawal of freshwater from the Suwannee River for human consumption is a possibility and could impact fish assemblages found in the estuary (Tsou and Matheson, 2002).

This article describes habitat-specific assemblages by examining the fish fauna collected in seagrass habi-

tats with those collected in tidal-creek habitats in the Suwannee River estuary. We performed comparisons of monthly collections of fish found along tidal-creek shorelines and those found in seagrass habitats to define fish assemblages and incorporated abiotic parameters as potential factors influencing the assemblages. We also compared length distributions of species in each habitat to examine the success of YOY recruitment and the subsequent influence of YOY recruitment on fish assemblages in order to understand the nursery function of each habitat.

Methods

Study location

This study took place in the Suwannee River estuary, which lies along the gulf coast of Florida, extending from just north of the Suwannee River to Cedar Key (Fig. 1). The Suwannee River empties directly into the Gulf of Mexico forming an unusual open estuary that stretches 13 kilometers north of the river mouth, southeastward to the islands of Cedar Key, and extends approximately 8 kilometers offshore (Leadon[1]). The Suwannee River estuary is shallow (water depth <2.2 m below mean sea level), and has semidiurnal tides with a tidal range of 0.7 m. The shoreline is relatively undeveloped; the city of Cedar Key (pop. 898) along the southeastern edge of the estuary and the small town of Suwannee approximately 4.8 kilometers inland along the Suwannee River are the only populated areas. The remainder of the coastline, consisting of the Lower Suwannee and Cedar Keys National Wildlife Refuges and the Cedar Key State Preserve, is owned by the public.

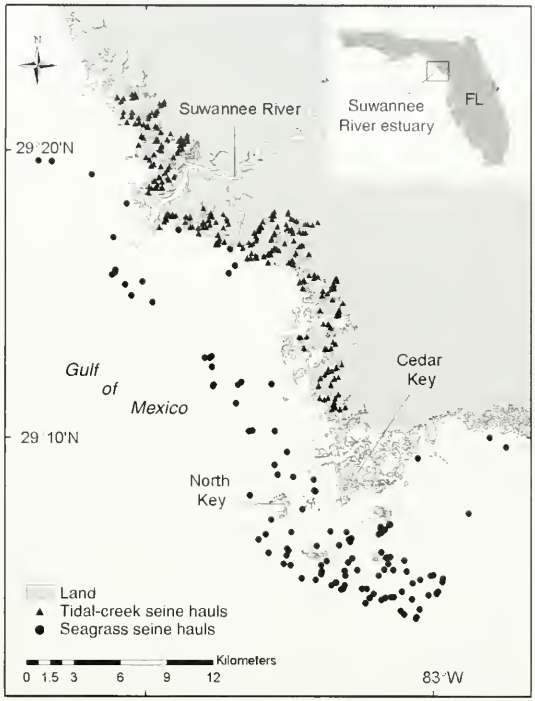

Figure 1

Study area showing location of tidal-creek and seagrass seine hauls in the Suwannee River estuary, located on the gulf coast of Florida.

Study design

Randomly selected sites were sampled monthly within tidal-creek and seagrass habitats from January 1997 through December 1999. Juvenile and small adult fish from each site were collected using a 21.3-m × 1.8-m nylon seine with 3.2-mm mesh and a center bag measuring 1.8-m × 1.8-m × 1.8-m. Sampling methods depended on the habitat sampled, and all seines were deployed during daylight hours.

Collections in tidal creeks consisted of six hauls per month in 1997 and increased to nine hauls per month in 1998 and 1999. Tidal creeks consisted of soft mud, deep channels, oyster bars, and steep banks. Shoreline vegetation included saltmarsh cord grass (*Spartina alterniflora*) and needle rush (*Juncus roemerianus*) near the creek mouths and changed to a variety of freshwater marsh grasses and terrestrial vegetation upstream. The seine was set from a boat in a semicircular pattern along the shoreline, retrieved onshore, and sampled an average area of 68 m^2 per haul. Shoreline areas inundated with vegetation were not sampled if the water depth was greater than 0.5 m in order to reduce the interference of vegetation during sample collections. Sampling in tidal-creeks was limited to the shoreline because the water was too deep in the channels to deploy the seine. In addition, despite the importance of oyster bar habitat, oyster bars located inside tidal creeks were not sampled because they interfered with the proper deployment of the seine.

Seagrass habitats generally surrounded the major islands near Cedar Key, including North Key and nearby islands (Fig. 1). In addition, vegetated patches extended from North Key northwestward to the mouth of the Suwannee River and were present in shallow areas approximately three kilometers west of the Suwannee River (Fig. 1). Dominant seagrass species in the Suwannee River estuary included turtle grass (*Thalassia testudi-*

[1] Leadon, C. J. 1979. Unpubl. manuscr. Environmental effects of river flows and levels in the Suwannee River subbasin below Wilcox and the Suwannee River estuary, Florida, 59 p. Suwannee River Water Management District Interim Report, 9225 County Road 49, Live Oak, FL 32060.

num), manatee grass (*Syringodium filliforme*), and shoal grass (*Halodule wrightii*). Percent coverage was estimated visually, or if water clarity was insufficient to visually inspect the bottom, bottom samples were collected at 3-m intervals during deployment of the seine. For analytical purposes, areas sampled had to contain at least ten percent seagrass to be considered seagrass habitat. Samples were classified as "vegetated" or "unvegetated" after sampling; and monthly collections varied from one to seven hauls per month depending on seagrass coverage. Seagrass habitats were sampled by pulling the seine into the current or wind, whichever was strongest. We kept the opening of the net at a constant width by maintaining tension on a 15.5-m line that was attached between each end pole of the seine while the seine was hauled for a distance of 9.1 m. The distance covered by the seine was measured by a weighted line from the starting point. The net was retrieved by bringing the end poles together and pulling the net at an angle around a vertical pole that closed the wings of the net and forced the catch into the bag. A typical seine haul over seagrass habitat covered approximately 140 m^2.

In the field, all fish were identified to the lowest possible taxon, counted, and released. Up to 40 individuals of species of special interest (important to the commercial or recreational fishery) and 10 individuals of all other species were measured to the nearest millimeter standard length (SL). For quality-control purposes, three specimens of each species collected were returned to the laboratory so that species identification could be confirmed. At each site, Secchi depth and water depth were measured, and water temperature (°C), salinity, dissolved oxygen level (mg/L), and pH were measured by using a Hydrolab Surveyor3® water-quality instrument (Hach Environmental, Loveland, CO).

Data analysis

Multivariate analyses were used to compare fish community structures along tidal-creek shorelines to those found in seagrass habitats (Field et al., 1982). Average monthly abundance estimates (number of fish divided by the number of hauls) were calculated separately for each fish species in each habitat type. Average monthly abundance estimates were then converted to percent composition to correct for bias introduced by the two different net-deployment methods and for the different levels of effort in each habitat. Fishes that were not identified to species were eliminated (<0.1% of total fish collected) except where species complexes, such as silversides (*Menidia* spp.), mojarras (*Eucinostomus* spp. <50 mm SL), menhaden (*Brevoortia* spp.), and minnows (*Notropis* spp.) were substituted. Species complexes were used when meristic characters for juveniles were insufficient to distinguish between two or more possible species (*Eucinostomus* spp. and *Notropis* spp.) or where there was possible hybridization (*Menidia* spp. and *Brevoortia* spp.).

Fish-community comparisons based on percent species composition by habitat and month were conducted by using algorithms in PRIMER (Plymouth Routines in Multivariate Ecological Research, vers. 5, Plymouth Marine Laboratory, UK) for the study of community structure (Clarke and Warwick, 1994). To identify fish assemblages, hierarchical agglomerative cluster analysis was performed with the Bray-Curtis similarity matrix calculated on fourth-root transformed percentage data. The fourth-root transformation reduced the dominance of abundant species and increased the influence of less abundant species in the community analysis. The cluster analysis was run on one matrix consisting of all transformed fish abundance estimates collected in tidal-creek and seagrass habitats combined.

To identify species that were responsible for the patterns observed in the cluster analysis, similarity and dissimilarity percentage breakdowns were conducted by using the SIMPER procedure in PRIMER (Clarke, 1993). Average similarities between assemblages were analyzed to determine the contribution of each species to the overall similarity. This procedure reduced the number of species required to explain the patterns observed in the cluster diagram and allowed for a simplified interpretation of the species assemblages. The higher the similarity value, the more alike samples were within assemblages. Alternatively, dissimilarity values were examined to identify species that were characteristic of a particular assemblage. Species that have high average dissimilarity values and low standard deviations are those that contribute consistently to samples within their group, with the result that they can be used to distinguish between groups.

The relationship between environmental variables and fish community structure was examined by using the BIO-ENV procedure. A Spearman rank correlation test was used to compare ranked values from the aforementioned biota similarity matrix to ranked values from an environmental similarity matrix, which was created from environmental variables measured in this study. Comparisons were based on normalized Euclidean distance. The environmental variables used to create the environmental similarity matrix included pH, water temperature, salinity, water depth, and Secchi depth. Dissolved oxygen was strongly correlated with water temperature and was therefore not included in the analysis because it would produce results similar to those produced by water temperature. Abiotic variables were standardized by subtracting each mean and dividing by the standard error to remove any bias associated with the different measurement scales.

The influence of recruitment of YOY fishes in defining fish assemblages was examined. By relating increases in abundance of species that were identified to be important contributors through the SIMPER procedure to decreases in their average length in both habitats, we were able to identify the timing of juvenile recruitment. Length-frequency distributions showed that the seine continued to catch larger individuals and therefore the decrease in average length was not due to a decrease

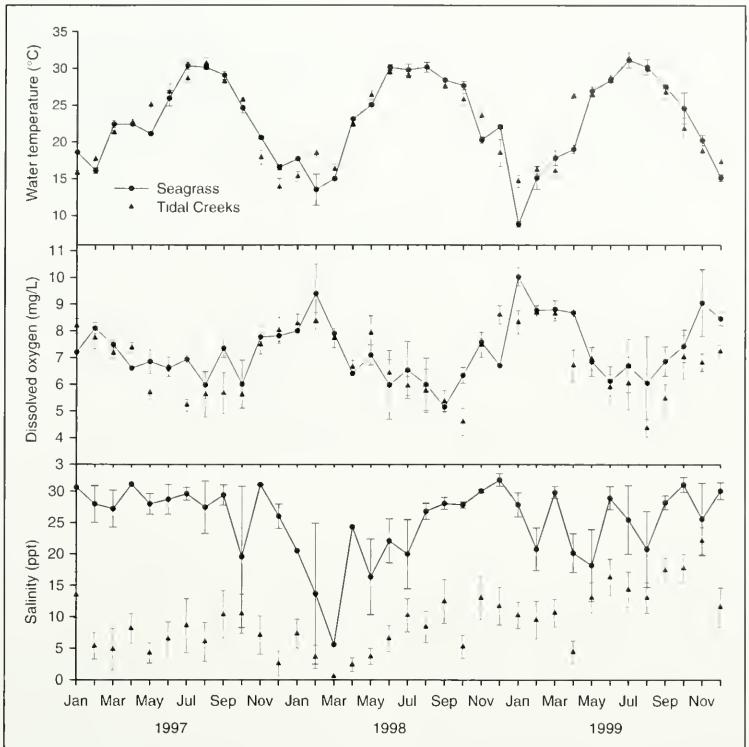

Figure 2

Monthly mean values (± standard error) for water temperature, dissolved oxygen, and salinity from January 1997 to December 1999. Circles represent values measured in seagrass habitats; triangles represent values measured in tidal-creek habitats.

in the number of larger fish. The mean length of each species in each sample was calculated by habitat, and differences in mean length were tested by using fish assemblages as the main factor in a one-way ANOVA. Multiple comparisons tests (Tukey's test) were then conducted to examine significant ANOVA results and these tests determined which assemblages contained fishes with significantly different lengths.

Results

Environmental conditions

The combination of water temperature, salinity, and water depth had the highest correlation (ρ_w=0.659) with the fish assemblages of any possible combination of measured abiotic variables. Seasonal patterns were observed for water temperature and dissolved oxygen, whereas salinity fluctuated in seagrass habitats and generally increased during 1999 in tidal-creek habitats (Fig. 2). Water temperatures ranged from 7.5° to 32.5°C (mean=23.0°C, SE=0.99) in the seagrass habitats and ranged from 10.3° to 33.3°C (mean=23.1°C, SE=0.91) in the tidal-creek habitats. Minimum values of dissolved oxygen coincided with the highest water temperatures in each habitat and ranged from 2.9 to 12.7 mg/L in the seagrass habitats and from 2.9 to 13.6 mg/L in the tidal-creek habitats. Salinity, however, was lower during all seasons in the tidal-creek habitats than in the seagrass habitats (Fig. 2). Mean salinity in the seagrass habitats was 27.1‰ (SE=0.91) and ranged from nearly fresh (1.3‰) to marine (34.8‰) depending on river discharge, whereas in the tidal creeks, mean salinity was 9.5‰ (SE=0.81) and ranged from 0.0‰ to 29.0‰. An unusually high period of rain during February and March of 1998 decreased salinity values in the tidal-creek and seagrass habitats.

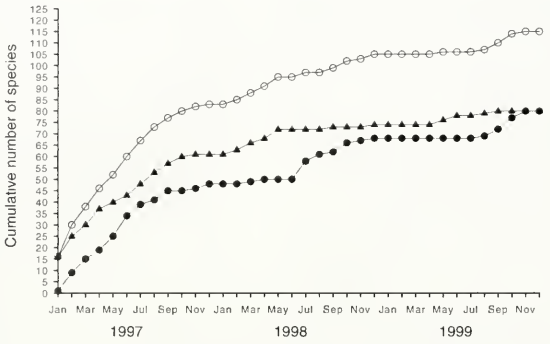

Figure 3

Cumulative number of species collected in both tidal-creek and seagrass habitats (open circles) and number of species collected in tidal-creeks (triangles) and seagrass habitats (filled circles) by year and month from January 1997 to December 1999.

Fish fauna

At the conclusion of the three-year study, 111 fish species and 4 additional species complexes had been collected. During the first year of the study, 61 species were collected in samples taken in tidal-creek habitats, and 48 species were collected in seagrass habitats (Fig. 3). Thirteen new species were added to the species list from tidal creek samples and 20 new species were added to the list from samples taken in seagrass habitats during 1998. During the final year of sampling only six additional species were collected in tidal creeks and 12 new species were collected in seagrass habitats. Overall, tidal creeks contained greater relative (uncorrected for gear efficiency) densities of fish (3.89 fish/m^2) compared with seagrass habitats (0.93 fish per m^2). In seagrass habitats, 15,395 individuals were collected in 118 samples that covered approximately 16,520 m^2 of seagrass habitat (Table 1). In tidal-creek habitats, a total of 76,176 individuals were collected from 288 samples that covered approximately 19,584 m^2 of tidal-creek shoreline habitat (Table 2). Thirty five species were restricted to seagrass habitats, and another 35 species were collected only in tidal creeks. The remaining 45 species were collected in both habitats at least once during the study. Overall, twelve families were restricted to seagrass habitats: phycid hakes (Phycidae), toadfishes (Batrachiodidae), batfishes (Ogcocephalidae), flyingfishes (Exocoetidae), cardinalfishes (Apogonidae), barracudas (Sphyraenidae), wrasses (Labridae), combtooth blennies (Blenniidae), mackerels (Scombridae), triggerfishes (Balistidae), boxfishes (Ostraciidae), and porcupinefishes (Diodontidae; Table 1). Seven families were restricted to tidal-creek habitats: minnows (Cyprinidae), sunfishes (Centrarchidae), killifishes (Cyprinodontidae), gars (Lepisosteidae), eagle rays (Myliobatidae), pikes (Esocidae), and livebearers (Poeciliidae; Table 2).

Fish assemblages

A clear separation of fish assemblages was identified and indicated by two main branches that corresponded to fishes found in seagrass habitats and those found in tidal-creek habitats (Fig. 4). There were two months identified from seagrass samples (January 1997 and March 1998) that had a species composition that was more closely linked to samples taken from tidal creeks.

Seagrass habitats

Seasonal fish assemblages in seagrass habitats were evident during all three years of the study, which included winter–spring, summer, and fall assemblages (Fig. 4). The winter–spring assemblage consisted principally of pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), dusky pipefish (*Syngnathus floridae*), southern puffer (*Sphoeroides nephelus*), and gulf pipefish (*Syngnathus scovelli*), which together accounted for more than 95% of the cumulative percent similarity. The summer assemblage had a higher average similarity value (43.67) than did the winter–spring assemblage (42.56) and consisted of more than 21 species. Eleven of these species—silver perch (*Bairdiella chrysoura*), *S. floridae*, bay anchovy (*Anchoa mitchilli*), *L. rhomboides*, *Eucinostomus* spp., spotted seatrout (*Cynoscion nebulosus*), *S. scovelli*, planehead filefish (*Monacanthus hispidus*), striped anchovy (*Anchoa hepsetus*), inshore lizardfish (*Synodus foetens*), and *O. chrysoptera*—accounted for more than 75% of the cumulative similarity of the summer assemblage. The fall assemblage had the high-

Table 1

Taxonomic list of individuals collected in seagrass habitats for each species by month and total number collected, all years combined.

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Dasyatidae	*Dasyatis sabina*	0	0	0	0	0	0	1	0	1	3	1	1	7
	Dasyatis say	0	0	0	0	0	2	0	0	0	0	0	0	2
Ophichthidae	*Myrophis punctatus*	0	0	0	1	0	0	0	0	0	0	0	0	1
Clupeidae	*Harengula jaguana*	0	0	0	0	0	0	6	230	0	162	0	0	398
	Brevoortia spp.	0	0	1	0	0	0	0	0	0	0	0	0	1
	Opisthonema oglinum	0	0	0	0	0	4	1	4	35	9	0	0	53
	Sardinella aurita	0	0	0	0	0	0	0	16	0	0	0	0	16
Engraulidae	*Anchoa hepsetus*	0	0	0	0	1	540	2	1	235	13	3	0	795
	Anchoa mitchilli	0	0	4	3	0	38	1567	3838	632	3504	53	0	9639
Ariidae	*Arius felis*	0	0	0	0	0	1	1	14	45	1	0	0	62
	Bagre marinus	0	0	0	0	0	0	0	0	1	0	0	0	1
Synodontidae	*Synodus foetens*	0	0	0	0	1	2	3	8	3	1	1	1	20
Gadidae	*Urophycis floridana*	0	0	0	0	0	0	0	0	0	0	0	6	6
Batrachiodidae	*Opsanus beta*	0	0	0	0	0	0	0	0	1	0	0	0	1
Ogcocephalidae	*Ogcocephalus radiatus*	0	0	0	1	0	0	0	0	0	0	0	0	1
Exocoetidae	*Hyporhamphus meeki*	0	0	0	0	1	7	2	0	0	0	0	0	10
Belonidae	*Strongylura marina*	0	0	0	0	0	1	3	1	0	0	0	0	5
Atherinidae	*Membras martinica*	0	10	0	0	1	10	49	21	13	15	3	0	122
	Menidia spp.	0	0	0	0	0	0	0	0	0	0	1	2	3
Syngnathidae	*Hippocampus erectus*	0	0	0	0	0	0	0	0	0	1	0	0	1
	Hippocampus zosterae	0	1	0	0	0	0	1	1	2	0	1	2	8
	Syngnathus floridae	2	7	1	9	2	34	33	53	48	26	52	38	305
	Syngnathus louisianae	0	0	0	1	0	3	4	2	1	4	3	0	18
	Syngnathus scovelli	0	3	6	4	0	11	32	4	9	10	13	13	105
Serranidae	*Mycteroperca microlepis*	0	0	0	0	0	0	0	0	0	1	0	0	1
	Centropristis striata	0	0	0	0	0	1	2	7	12	3	74	12	111
	Serraniculus pumilio	0	0	0	0	0	0	0	0	0	0	10	0	10
	Serranus subligarius	0	0	0	0	0	0	0	0	2	0	0	0	2
Apogonidae	*Astrapogon alutus*	0	0	0	0	0	0	0	0	0	1	0	0	1
Carangidae	*Caranx hippos*	0	0	0	0	0	0	0	0	0	2	0	0	2
	Chloroscombrus chrysurus	0	0	0	0	0	0	2	12	5	0	0	0	19
	Oligoplites saurus	0	0	0	0	0	7	2	2	4	2	0	0	17
	Selene vomer	0	0	0	0	0	0	0	0	0	2	0	0	2
Lutjanidae	*Lutjanus griseus*	0	0	0	0	0	0	0	1	0	1	0	0	2
	Lutjanus synagris	0	0	0	0	0	0	3	0	0	1	2	0	6
Gerreidae	*Eucinostomus gula*	0	0	0	0	0	0	0	0	6	6	4	1	17
	Eucinostomus harengulus	0	0	0	0	0	1	0	2	1	0	0	0	4
	Eucinostomus spp.	0	0	0	0	0	34	172	162	73	13	54	36	544
Haemulidae	*Haemulon plumieri*	0	0	0	0	0	0	1	6	11	4	3	7	32
	Orthopristis chrysoptera	1	0	6	26	738	30	38	0	8	4	0	1	852
Sparidae	*Diplodus holbrooki*	0	0	0	0	7	17	0	4	1	7	0	0	36
	Lagodon rhomboides	17	65	63	87	21	54	24	27	40	36	32	87	553
Sciaenidae	*Bairdiella chrysoura*	0	0	0	3	24	159	273	59	184	44	2	1	749
	Cynoscion arenarius	0	0	0	0	0	0	1	24	0	0	0	0	25
	Cynoscion nebulosus	0	0	0	0	0	4	70	37	10	6	1	0	128
	Leiostomus xanthurus	2	34	1	0	0	0	0	0	2	0	0	0	39
	Menticirrhus americanus	0	0	0	0	0	2	13	119	2	0	1	0	137

continued

Table 1 (continued)

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Sciaenidae (cont.)	*Menticirrhus saxatilis*	0	0	1	0	0	7	0	5	0	0	0	2	15
	Sciaenops ocellatus	0	0	0	0	0	0	0	0	0	0	9	0	9
Ephipidae	*Chaetodipterus faber*	0	0	0	0	0	0	2	12	2	0	0	0	16
Mugilidae	*Mugil cephalus*	0	5	1	0	0	0	0	0	0	0	0	0	6
	Mugil curema	0	0	0	1	0	0	0	0	0	0	0	0	1
Sphyraenidae	*Sphyraena borealis*	0	0	0	0	4	0	0	0	0	0	0	0	4
Labridae	*Halichoeres bivittatus*	0	0	0	0	0	0	0	3	0	0	0	0	3
	Lachnolaimus maximus	0	0	0	0	0	0	0	0	2	1	0	0	3
Blenniidae	*Chasmodes saburrae*	0	0	0	0	0	0	9	0	5	0	2	0	16
	Parablennius marmoreus	0	0	0	0	0	0	0	1	0	0	1	0	2
	Hypsoblennius hentzi	0	0	0	0	0	0	0	0	1	0	0	2	3
	Hypleurochilus geminatus	0	0	0	0	0	0	2	0	0	0	0	0	2
Gobiidae	*Gobionellus boleosoma*	0	0	0	0	0	0	9	0	0	0	0	0	9
	Gobiosoma bosc	0	0	0	0	0	0	29	0	0	0	1	0	30
	Gobiosoma longipala	0	0	0	0	0	0	0	0	0	1	0	0	1
	Gobiosoma robustum	0	0	0	2	0	0	7	2	0	1	0	1	13
	Microgobius gulosus	0	0	0	0	0	0	3	2	0	0	2	0	7
	Microgobius thalassinus	0	0	0	0	0	0	0	77	0	0	0	0	77
Scombridae	*Scomberomorus maculatus*	0	0	0	0	0	0	0	0	1	0	0	0	1
Triglidae	*Prionotus scitulus*	0	2	0	0	0	2	5	4	2	1	0	1	17
	Prionotus tribulus	0	0	0	0	0	0	0	2	0	0	1	0	3
Bothidae	*Paralichthys albigutta*	0	0	2	2	0	0	2	0	2	0	0	0	8
	Etropus crossotus	0	3	1	0	0	0	2	1	1	0	0	1	9
	Etropus microstomus	0	0	1	0	0	0	0	0	0	0	0	0	1
Cynoglossidae	*Symphurus plagiusa*	0	0	1	0	0	1	1	9	0	0	0	1	13
Soleidae	*Achirus lineatus*	0	0	0	0	0	0	1	7	0	0	0	0	8
	Trinectes maculatus	0	0	0	0	0	0	0	0	1	0	0	0	1
Balistidae	*Aluterus schoepfi*	0	0	0	0	0	1	1	2	0	1	0	0	5
	Monacanthus ciliatus	0	0	0	0	0	0	0	2	10	8	2	19	41
	Monacanthus hispidus	0	0	0	0	2	10	1	36	3	9	7	25	93
Ostraciidae	*Lactophrys quadricornis*	0	0	2	0	0	2	0	6	6	3	3	1	23
Tetraodontidae	*Sphoeroides nephelus*	0	0	2	16	4	2	2	2	1	4	2	2	37
Diodontidae	*Chilomycterus schoepfi*	0	1	2	0	4	2	0	11	5	10	5	9	49
Column total		22	131	95	156	810	989	2382	4839	1429	3921	349	272	15,395
Number of hauls		6	10	9	4	5	15	10	11	11	11	10	16	118

est average similarity level at 48.90, and nine species—*S. floridae*, *M. hispidus*, black seabass (*Centropristis striata*), *L. rhomboides*, *Eucinostomus* spp., fringed filefish (*Monacanthus ciliatus*), *S. scovelli*, striped burrfish (*Chilomycterus schoepfi*), and *S. nephelus*—accounted for more than 91% of the cumulative similarity. *Lagodon rhomboides* and *S. floridae* were characteristic of all three assemblages, and *Eucinostomus* spp., *S. scovelli*, and *M. hispidus* were important contributors to the summer and fall assemblages. Other abundant species from seagrass assemblages included southern kingfish (*Menticirrhus americanus*), rough silverside (*Membras martinica*), and gobiids, particularly green goby (*Microgobius thalassinus*) and naked goby (*Gobiosoma bosc*).

A significant drop in salinity during March 1998 corresponded to an alteration in the fish community collected in seagrass habitats. The species present in the seagrass habitats during March 1998 were more consistent with species collected in tidal creeks and included *A. mitchilli*, *Brevoortia* spp., and spot (*Leiostomus xanthurus*), none of which were collected in March of 1997 or 1999 in seagrass habitats. Samples collected during March 1997 and 1999 contained individuals more characteristic of seagrass habitats, such as *C. schoepfi*, *L. rhomboides*, *O. chrysoptera*, and *S. nephelus* in 1997 and scrawled cowfish (*Acanthostracion quadricornis*), *O. chrysoptera*, *L. rhomboides*, *S. floridae*, and *S. scovelli* in 1999.

Table 2

Taxonomic list of individuals collected in tidal-creeks for each species by month and total number collected, all years combined.

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Dasyatidae	*Dasyatis sabina*	0	0	6	1	1	0	0	0	1	1	3	0	13
Myliobatidae	*Rhinoptera bonasus*	0	0	0	0	3	0	0	0	0	0	0	0	3
Lepisosteidae	*Lepisosteus osseus*	0	0	0	0	0	2	2	1	0	0	0	0	5
	Lepisosteus platyrhincus	0	0	1	1	0	1	1	0	2	2	0	0	8
Ophichthidae	*Myrophis punctatus*	0	0	0	0	1	0	0	0	0	0	0	0	1
Clupeidae	*Harengula jaguana*	0	0	0	0	2	1	2	9	10	2	0	0	26
	Brevoortia spp.	15	139	93	400	394	7	5	0	0	0	0	1	1054
	Sardinella aurita	0	0	0	0	0	0	22	0	0	0	0	0	22
Engraulidae	*Anchoa hepsetus*	3	0	0	1	175	482	71	33	7	0	3	0	775
	Anchoa mitchilli	86	497	825	108	612	3298	10,329	6970	5776	7436	1637	2107	39,681
Cyprinidae	*Notemigonus crysoleucas*	0	2	1	0	0	0	0	0	0	0	0	0	3
	Notropis spp.	0	0	0	0	4	9	0	0	0	0	0	0	13
Ariidae	*Arius felis*	0	0	0	0	0	0	0	2	3	0	0	0	5
Esocidae	*Esox niger*	0	0	0	1	1	0	0	0	0	0	0	0	2
Synodontidae	*Synodus foetens*	0	0	0	3	7	0	0	0	1	0	3	1	15
Belonidae	*Strongylura marina*	0	0	0	2	4	1	8	1	1	1	0	0	18
	Strongylura notata	2	0	0	0	0	0	3	2	8	0	1	0	16
	Strongylura timucu	0	0	0	0	11	1	8	3	11	0	0	0	34
Cyprinodontidae	*Adinia xenica*	7	7	0	4	1	0	12	23	0	153	14	25	246
	Cyprinodon variegatus	4	0	0	1	0	0	0	0	0	0	2	3	10
	Lucania goodei	0	0	11	0	0	0	0	0	0	0	0	0	11
	Lucania parva	0	2	2	0	0	1	2	15	4	0	0	6	32
Fundulidae	*Fundulus confluentus*	2	0	0	0	0	0	0	0	0	1	0	3	6
	Fundulus grandis	33	39	6	28	9	30	21	127	9	39	170	218	729
	Fundulus majalis	29	12	24	7	0	18	0	42	3	10	13	65	223
	Fundulus seminolis	7	2	0	1	0	14	0	14	5	6	0	1	50
Poeciliidae	*Gambusia holbrooki*	6	0	59	2	4	1	0	1	12	4	1	7	97
	Heterandria formosa	0	1	0	0	0	0	0	0	0	1	0	0	2
	Poecilia latipinna	1	0	0	0	2	2	0	17	0	4	4	12	42
Atherinidae	*Membras martinica*	0	0	4	0	9	566	2286	28	114	7	1	0	3015
	Menidia spp.	383	429	201	265	145	695	982	571	814	602	749	358	6194
Syngnathidae	*Syngnathus floridae*	0	1	0	0	0	0	0	0	1	0	0	0	2
	Syngnathus louisianae	0	0	0	0	0	0	0	0	1	0	1	0	2
	Syngnathus scovelli	2	1	2	0	1	0	1	7	5	1	2	11	33
Serranidae	*Diplectrum bivittatum*	0	0	0	0	0	0	0	0	0	0	1	0	1
Centrarchidae	*Enneacanthus gloriosus*	0	0	2	0	0	0	0	0	0	0	0	0	2
	Elassoma zonatum	0	0	0	0	4	0	0	0	0	0	0	0	4
	Lepomis gulosus	0	1	1	0	0	0	0	0	0	0	0	0	2
	Lepomis macrochirus	0	0	0	0	0	0	0	0	1	0	0	0	1
	Lepomis marginatus	0	0	0	1	0	0	0	0	0	0	0	0	1
	Lepomis microlophus	0	0	0	0	1	0	0	0	0	0	0	0	1
	Lepomis punctatus	1	0	0	1	1	1	2	2	3	2	0	0	13
	Micropterus salmoides	0	0	3	1	14	4	0	5	8	2	0	0	37
Carangidae	*Chloroscombrus chrysurus*	0	0	0	0	0	0	1	3	15	2	0	0	21
	Oligoplites saurus	0	0	0	0	0	8	53	25	47	17	6	0	156
	Trachinotus falcatus	0	0	0	0	0	0	0	0	0	3	0	0	3

continued

Table 2 (continued)

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Lutjanidae	*Lutjanus griseus*	0	0	0	0	0	2	2	9	8	6	2	1	30
Gerreidae	*Eucinostomus gula*	1	0	0	0	0	0	0	4	7	25	49	3	89
	Eucinostomus harengulus	0	25	5	2	6	3	41	150	88	100	65	45	530
	Eucinostomus spp.	17	38	6	1	1	87	1035	1082	503	862	691	358	4681
Haemulidae	*Orthopristis chrysoptera*	0	0	0	0	0	0	0	2	0	0	0	0	2
Sparidae	*Archosargus probatocephalus*	7	1	1	0	1	1	0	1	0	0	1	0	13
	Lagodon rhomboides	87	231	146	142	67	114	111	85	38	29	53	10	1113
Sciaenidae	*Bairdiella chrysoura*	0	0	7	7	200	154	58	246	117	4	3	0	796
	Cynoscion arenarius	0	0	0	5	236	102	90	91	46	76	5	0	651
	Cynoscion nebulosus	3	1	1	0	5	11	21	53	62	23	36	2	218
	Leiostomus xanthurus	9526	2044	834	771	274	42	125	24	6	5	2	31	13,684
	Menticirrhus americanus	0	0	0	0	3	12	50	36	12	10	5	0	128
	Micropogonias undulatus	4	4	0	5	2	0	0	0	1	0	6	2	24
	Pogonias cromis	0	0	0	0	2	2	0	3	0	1	0	1	9
	Sciaenops ocellatus	26	28	20	15	3	7	4	1	1	48	105	65	323
Ephipidae	*Chaetodipterus faber*	0	0	0	0	0	1	3	1	3	0	0	0	8
Mugilidae	*Mugil cephalus*	175	159	59	25	2	39	22	7	18	1	6	6	519
	Mugil curema	1	0	0	0	0	25	2	0	0	0	0	1	29
	Mugil gyrans	0	0	0	0	0	0	0	0	2	0	0	4	6
Gobiidae	*Bathygobius soporator*	0	0	0	4	0	0	2	1	18	5	6	3	39
	Gobionellus boleosoma	0	0	3	6	9	0	1	6	15	0	4	0	44
	Gobiosoma bosc	8	3	14	7	1	40	21	17	52	20	18	67	268
	Gobiosoma robustum	0	6	3	1	0	8	7	10	6	0	4	15	60
	Microgobius gulosus	5	23	7	5	4	7	0	25	5	8	3	14	106
	Microgobius thalassinus	0	0	0	0	0	0	1	1	1	0	1	0	4
Triglidae	*Prionotus scitulus*	0	0	0	0	0	1	0	0	0	0	0	0	1
	Prionotus tribulus	0	0	0	1	0	0	0	0	1	11	4	0	17
Bothidae	*Paralichthys albigutta*	5	1	0	0	0	2	0	0	1	0	0	0	9
	Paralichthys lethostigma	0	0	1	0	0	1	0	0	0	0	0	0	2
	Etropus crossotus	0	0	0	0	0	1	0	0	0	0	0	0	1
Cynoglossidae	*Symphurus plagiusa*	6	0	0	0	0	2	2	1	13	5	1	5	35
Soleidae	*Achirus lineatus*	0	0	0	0	0	2	4	9	10	8	2	0	35
	Trinectes maculatus	1	8	10	0	5	13	1	13	2	4	2	1	60
Tetraodontidae	*Sphoeroides nephelus*	0	0	0	1	6	0	0	0	0	4	0	1	12
Column total		10,453	3705	2358	1826	2233	5821	15,414	9779	7898	9551	3685	3453	76,176
Number of hauls		24	24	24	24	24	24	24	24	24	24	24	24	288

Recruitment of YOY fishes had an influence on defining fish assemblages in seagrass habitats. The winter–spring assemblage was dominated by YOY *L. rhomboides* and *O. chrysoptera* (Table 3), which had significantly shorter standard lengths than did the other assemblages (Table 4). The summer assemblage showed an increase in the number of species and an increase in their abundance, but there were no significant differences in length for YOY for any species between assemblages.

Tidal-creek habitats

Three fish assemblages (winter–spring, summer, and fall) were identified from samples taken in tidal-creek habitats and reflected similar seasonal patterns compared with fish assemblages identified from seagrass habitats (Fig. 4). The winter–spring assemblage had an average similarity level of 51.76 and consisted of *L. xanthurus*, *Menidia* spp., *A. mitchilli*, *L. rhomboides*, *M. cephalus*, and red drum (*Sciaenops ocellatus*). These six

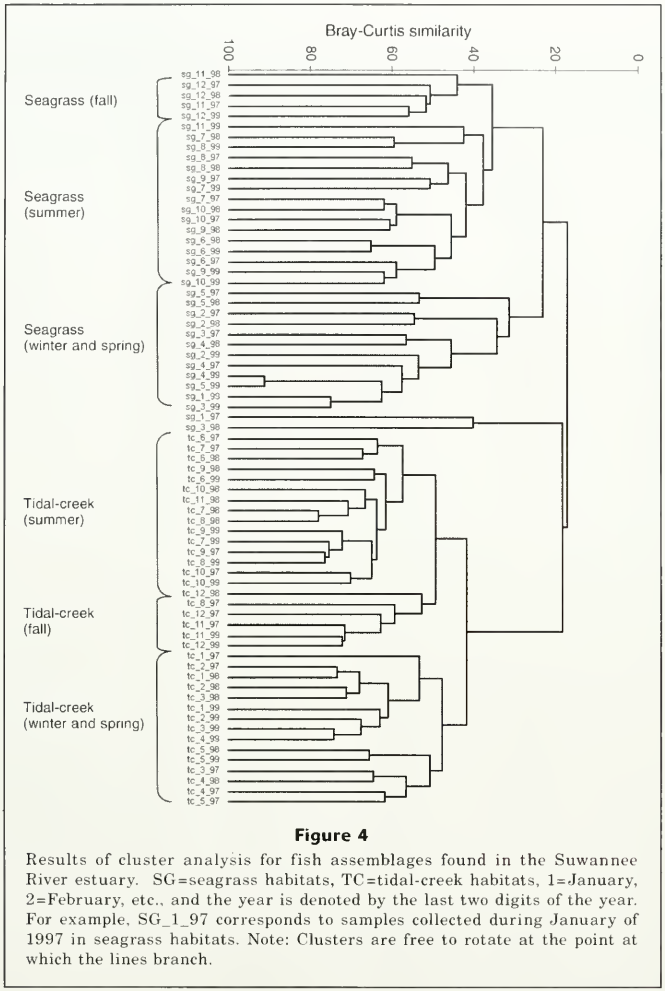

Figure 4

Results of cluster analysis for fish assemblages found in the Suwannee River estuary. SG=seagrass habitats, TC=tidal-creek habitats, 1=January, 2=February, etc., and the year is denoted by the last two digits of the year. For example, SG_1_97 corresponds to samples collected during January of 1997 in seagrass habitats. Note: Clusters are free to rotate at the point at which the lines branch.

species accounted for more than 68% of the cumulative similarity within the winter–spring assemblage. The summer assemblage had an average similarity level of 62.29 and was characterized by ten species that accounted for 70.65% of the cumulative similarity: *A. mitchilli*, *Menidia* spp., *Eucinostomus* spp., sand seatrout (*Cynoscion arenarius*), *B. chrysoura*, *C. nebulosus*, *L. rhomboides*, *E. harengulus*, *M. martinica*, and leatherjacket (*Oligoplites saurus*). The fall assemblage had an average similarity level of 60.36 and was characterized by *Eucinostomus* spp., *Menidia* spp., gulf killifish (*Fundulus grandis*), *A. mitchilli*, *E. harengulus*, diamond killifish (*Adinia xenica*), clown goby (*Microgobius gulosus*), and *M. cephalus*, which accounted for more than 67% of the cumulative similarity. Species tolerant of low salinity, such as *A. xenica*, marsh killifish (*Fundulus confluentus*), mosquitofish (*Gambusia holbrooki*), and least killifish (*Heterandria formosa*) were commonly collected in tidal creeks. There were 35 species collected, including groups such as cyprinids, cyprinodontids, poeciliids, lepisosteids, and centrarchids, which were restricted entirely to tidal creeks (Table 2).

Seasonal recruitment of juvenile fishes to tidal-creek habitats was evident and remained consistent throughout the study resulting in three clearly defined assemblages. Young-of-the-year *L. xanthurus* recruited to

Table 3

Results of SIMPER procedure showing the average percent dissimilarity (δ%) for important species between seagrass assemblages. δi is the average contribution of the ith species to the disssimilarity between groups; δi/SD(δi) is the ratio between the average contribution of the i^{th} species and the standard deviation of δi; Cum δi% is the cumulative contribution to the total dissimilarity. Species are listed in decreasing contribution to average dissimilarity.

Species	Average abundance		δi	δi/SD(δi)	δi%	Cumulative δi%
	winter–spring	summer				
Eucinostomus spp.	0.24	9.9	4.8	1.38	6.31	6.31
Lagodon rhomboides	10.75	1.83	4.5	1.69	5.91	12.22
Bairdiella chrysoura	1.01	12.76	4.38	1.25	5.75	17.97
Orthopristis chrysoptera	26.58	0.94	3.66	1.17	4.81	22.78
Monacanthus hispidus	0.09	1.89	3.25	1.22	4.27	27.05
Syngnathus floridae	1.2	3.88	3.24	1.1	4.25	31.3
Centropristis striata	0.01	1.82	2.68	0.99	3.52	34.82
Anchoa hepsetus	0.03	11.95	2.67	0.8	3.51	38.33
Syngnathus scovelli	0.8	1.13	2.48	1.36	3.25	41.58
Sphoeroides nephelus	1.24	0.19	2.27	1.2	2.99	44.57
Anchoa mitchilli	0.33	4.46	2.27	0.95	2.98	47.55
Chilomycterus schoepfi	0.18	0.46	2.12	1.07	2.78	50.33
	winter–spring	fall				
Anchoa mitchilli	0.33	478.1	10.87	2.32	13.31	13.31
Lagodon rhomboides	10.75	4.57	6.43	1.36	7.87	21.18
Orthopristis chrysoptera	26.58	1.33	4.73	1.05	5.79	26.97
Bairdiella chrysoura	1.01	8.26	3.39	1.58	4.15	31.12
Leiostomus xanthurus	0.67	0.14	3.26	0.61	3.99	35.11
Syngnathus scovelli	0.8	0.71	2.83	1.19	3.46	38.57
Syngnathus floridae	1.2	3.26	2.81	1.27	3.44	42.01
Eucinostomus spp.	0.24	5.38	2.68	1.24	3.28	45.29
Harengula jaguana	0	9.74	2.57	1.24	3.15	48.44
Sphoeroides nephelus	1.24	0.12	2.55	0.91	3.12	51.56
	summer	fall				
Anchoa mitchilli	4.46	478.1	6.13	1.98	9.30	9.30
Eucinostomus spp.	9.9	5.38	3.11	1.34	4.72	14.02
Bairdiella chrysoura	12.76	8.26	2.70	1.21	4.10	18.12
Anchoa hepsetus	11.95	0.48	2.36	0.98	3.59	21.71
Syngnathus floridae	3.88	3.26	2.35	1.05	3.56	25.27
Monacanthus hispidus	1.89	0.38	2.34	1.14	3.55	28.82
Harengula jaguana	2.79	9.74	2.15	1.25	3.27	32.09
Centropristis striata	1.82	0.64	2.06	1.01	3.13	35.22
Syngnathus scovelli	1.13	0.71	1.82	1.35	2.77	37.99
Lagodon rhomboides	1.83	4.57	1.75	1.08	2.65	40.64
Chilomycterus schoepfi	0.46	0.52	1.72	1.13	2.61	43.25
Cynoscion nebulosus	1.54	1.95	1.66	1.31	2.53	45.78
Monacanthus ciliatus	0.45	0.45	1.62	0.83	2.47	48.25
Orthopristis chrysoptera	0.94	1.33	1.62	1.04	2.46	50.71

Table 4

Results of ANOVA comparing standard length of each species between habitats and seasonal assemblages identified through PRIMER. * <0.05, ** <0.01, *** <0.001.

Species	Factor	df	*F*	*P*	Tukey HSD
Bairdiella chrysoura	habitat	1	0.02	0.8750	
	season	2	0.38	0.6819	
Cynoscion nebulosus	habitat	1	2.74	0.1008	
	season	2	8.03	***	winter > summer
Lagodon rhomboides	habitat	1	6.61	*	tidal-creek > seagrass
	season	2	80.12	***	summer > fall > winter
Leiostomus xanthurus	habitat	1	6.84	*	
	season	2	29.87	***	summer > fall, winter
Mugil cephalus	habitat	1	1.23	0.2713	
	season	2	2.54	0.0862	
Orthopristis chrysoptera	habitat	1	2.96	0.0996	
	season	2	4.6	*	summer > winter
Sciaenops ocellatus	habitat	1	1.98	0.1633	
	season	2	6.28	**	summer, winter > fall

tidal creeks and dominated samples collected during January and February (Tables 2 and 5). Recruitment of YOY *L. rhomboides* and *C. arenarius* also contributed to the winter-spring species assemblage (Tables 4 and 5). The summer assemblage was influenced by recruitment of YOY *F. grandis* and *C. nebulosus*, which had significantly shorter standard lengths than they had in the winter-spring assemblage. The recruitment of *S. ocellatus* helped to characterize the fall assemblage. Emigration of larger individuals could also account for a decrease in mean length; however length-frequency plots showed that larger individuals remained vulnerable to the gear and that the reduction in mean length was due to recruitment of YOY fishes.

Discussion

Fishes collected in seagrass habitats in this study were similar to those found in other studies of seagrass habitats; resident species were present year-round and there were seasonal pulses of juveniles that used the seagrass habitats as a nursery (Reid, 1954; Livingston, 1982; Weinstein and Brooks, 1983). The assemblages we identified were the result of the staggered influx of YOY fishes of different species to seagrass habitats throughout the year. For example, YOY *L. rhomboides* and *O. chrysoptera* recruited during winter and spring, whereas other abundant species such as YOY *B. chrysoura* and *Eucinostomus* spp. entered the nursery during summer and fall. We found an increase in species abundance and species richness during summer and fall similar to that found by Reid (1954), who conducted his study near Cedar Key. The same pattern was evident in other estuarine systems (Cowan and Birdsong, 1985; Rooker et al., 1998), demonstrating that recruitment of many juvenile fish species to seagrass habitats during summer and fall allows the juveniles to use the protection provided by the growing seagrasses (Stoner, 1983) and to use the food resources found within them (Carr and Adams, 1973).

Early-life-history stages of species with commercial or recreational importance were found in each habitat, but seagrass habitats contained a greater variety of juveniles from offshore reef species than did tidal creeks. Along the southeastern United States, juveniles of many economically important species use a variety of habitats in estuaries as nurseries, including mangroves, oyster reefs, marshes, tidal creeks, and seagrass habitats (Coleman et al., 1999, Coleman, et al., 2000). In our study, YOY reef fish taxa, such as serranids, lutjanids, and haemulids, were more abundant in seagrass habitats than they were in tidal-creek habitats, except for gray snapper (*Lutjanus griseus*). Juveniles of several reef species (*C. striata, Mycteroperca microlepis, Serraniculus pumilio, Serranus subligaris,* and *Lachnolaimus maximus*) were found only in seagrass habitats. However, a complicating factor in our study was the elimination of oyster habitats from our sampling design. Oyster reefs are known to harbor juvenile *C. striata* and *M. microlepis* (Coleman et al., 2000) and they may have been under-estimated in our study because we did not sample these habitats. Other economically important species, such as *C. nebulosus*, also recruited to the seagrass habitats and are known to reside in them much of their life (Reid, 1954; McMichael and Peters, 1989; Mason and Zengel, 1996). These economically important species use seagrass habitats in the Suwannee River estuary as a nursery and eventually enter local fisheries. Consequently, the maintenance of healthy

Table 5

Results of SIMPER procedure showing the average percent dissimilarity ($\delta\%$) for important species between tidal-creek assemblages. δi is the average contribution of the i^{th} species to the disssimilarity between groups; $\delta i/SD(\delta i)$ is the ratio between the average contribution of the i^{th} species and the standard deviation of δi; Cum $\delta i\%$ is the cumulative contribution to the total dissimilarity. Species are listed in decreasing contribution to average dissimilarity.

Species	Average abundance		δi	$\delta i/SD(\delta i)$	$\delta i\%$	Cumulative $\delta i\%$
	winter–spring	summer				
Leiostomus xanthurus	177.1	8.43	4.17	2.07	7.03	7.03
Anchoa mitchilli	4.93	243.61	3.83	2.4	6.46	13.49
Brevoortia spp.	10.87	0.74	2.65	1.42	4.46	17.95
Eucinostomus spp.	0.24	22.28	2.62	1.74	4.42	22.37
Cynoscion arenarius	1.62	3.02	1.94	1.77	3.26	25.63
Mugil cephalus	4.52	0.88	1.91	1.57	3.21	28.84
Membras martinica	0.04	21.61	1.9	1.10	3.19	32.03
Lagodon rhomboides	6.46	2.92	1.83	1.46	3.08	35.11
	winter–Spring	fall				
Leiostomus xanthurus	177.1	0.96	4.33	2.32	7.85	7.85
Eucinostomus spp.	0.24	24.63	4.03	2.63	7.30	15.15
Brevoortia spp.	10.87	0.03	2.58	1.41	4.68	19.83
Eucinsotomus herengulus	0.07	2.86	2.51	2.73	4.56	24.39
Fundulus grandis	1.26	12.02	2.19	1.72	3.97	28.36
Fundulus majalis	0.77	3.47	1.66	1.40	3.02	31.38
Adinia xenica	0.23	1.82	1.62	1.55	2.94	34.32
Cynoscion nebulosus	0.07	1.16	1.60	1.68	2.90	37.22
	summer	fall				
Fundulus grandis	1.16	12.02	2.59	2.34	4.84	4.84
Anchoa mitchilli	243.61	14.92	2.52	1.69	4.70	9.54
Sciaenops ocellotus	0.53	5.36	2.09	1.39	3.91	13.45
Eucinostomus spp.	22.28	24.63	1.89	1.27	3.53	16.98
Fundulus majalis	0.26	3.47	1.88	1.45	3.51	20.49
Bairdiella chrysoura	4.06	1.53	1.81	1.71	3.38	23.87
Adinia xenica	0.97	1.82	1.76	1.9	3.28	27.15
Cynoscion arenarius	3.02	0.87	1.7	1.78	3.18	30.33

seagrasses in this area is important to the preservation of these resources.

Tidal-creek habitats in the Suwannee River estuary provided resources for many species that had restricted distributions related to salinity tolerances and included taxa that were also found in the nearby seagrass habitats. We found recreationally important freshwater taxa, such as *Micropterus salmoides* and *Lepomis punctatus*, in tidal-creek habitats. Other groups restricted to tidal-creeks were those tolerant of low salinity and included the fundulids, poeciliids, and cyprinodontids. In addition, some economically valuable species were more abundant in tidal-creeks than in seagrass habitats, including *M. cephalus*, *C. arenarius*, *S. ocellatus*, and *L. griseus*. Tidal creeks also supported a greater density of fishes than did seagrass habitats—a density that could have resulted from habitat preferences, differential mortality between habitat types, or gear avoidance. Because the seine was set along the shoreline in tidal creeks, fishes were trapped between the seine and the shoreline, perhaps making them more vulnerable to the gear, whereas in seagrass habitats, the seine was pulled along the bottom with the end open prior to retrieval and fishes could have used the opening to escape.

The results of our study showed that there was a more consistent assemblage of fishes in tidal creeks, whereas

fish assemblages found in seagrass habitats had greater variability in the species present and in the abundance of those species. The more consistent assemblage of fishes found in tidal creeks could be explained by the persistence of vegetation throughout the year in tidal creeks, which may have contributed to reduced predation and may have provided direct or indirect sources of food. Vegetation coverage in seagrass habitats was seasonal and Strawn (1961) found that above-ground seagrass biomass declined during winter and increased during summer and fall. The increased complexity resulting from blade density and seagrass species heterogeneity offered by the growing seagrasses is known to affect fish abundance and composition (Stoner, 1983). The fish community structure in our study reflected this seasonal change; fewer fish species were present during winter and spring than in summer and fall. As seagrass biomass increased, fish species composition and total numbers also increased, resulting in greater variability within seagrass fish assemblages.

We found that the combination of water temperature, salinity, and water depth, more than any other combination of abiotic variables, helped to explain the fish community structure found in the Suwannee River estuary. Although water temperatures between the two habitats were similar, tidal creeks typically had soft mud sediments instead of sand and mud, marsh-grass species instead of submerged aquatic vegetation, deeper average depths, and lower salinity values. Water temperature has been shown to correlate with timing of recruitment for YOY fishes, which is ultimately related to adult spawning patterns (Subrahmanyam and Coultas, 1980; Nelson, 1998; Paperno, 2002). Because water temperatures were similar in each habitat, differences in fish-community structures were more likely related to salinity tolerances, factors that correlate with salinity and water depth. Water depth in the Suwannee River estuary varies seasonally; lowest water levels occur during winter (Strawn, 1961). The result is a confounding effect of water temperature and water depth that probably act in concert to limit distribution of fishes. A strong indicator that salinity may be the major abiotic factor that determines fish distributions, and ultimately species assemblages, was the low-salinity event during March 1998 that changed the seagrass fish assemblage to one more closely resembling a tidal-creek assemblage. If vegetation type were the primary factor controlling species assemblages in these habitats, tidal-creek species would remain in tidal-creeks and not invade seagrass habitats when salinity values changed to more favorable conditions. Therefore, varying salinities allowed different groups of fishes to use habitats according to their salinity tolerance (Wagner, 1999).

Nordlie (2003) examined 20 studies of estuarine salt marsh fish communities in eastern North America and characterized communities based on the life history patterns exhibited by the species. General life history categories were originally established by McHugh (1967) and included permanent residents, marine nursery, marine transients, diadromous, and freshwater transients. The 45 species that had overlapping distributions among habitats in our study were consistent with the classifications for marine nursery or marine transient species. Marine transient species do not require estuarine habitats for development, but venture into estuaries during periods of low rainfall, whereas marine nursery species require estuarine conditions for development. The two exceptions in our study (*Gobionellus bolesoma* and *M. gulosus*) were considered primary residents of saltmarsh communities, but were frequently found in estuaries.

We collected 80 fish species in tidal creeks in the Suwannee River estuary—more species than have been found in most other studies of tidal creeks—and this number could be related to the long-term duration of sampling. For example, Peterson and Turner (1994) observed 29 fish species inhabiting Louisiana marshes in a one-year study, whereas we found 51 additional species in our tidal-creek habitats. Similarly, Hettler (1989) found 35 species in a one-year study of saltmarsh fishes in North Carolina, and Weinstein (1979) recorded 61 species from his one-year study of the Cape Fear River, North Carolina. Furthermore, Cain and Dean (1976) found 51 species in a one-year examination of fishes in an intertidal creek in South Carolina. The first year of our study resulted in the collection of 61 species from tidal-creek habitats. It is likely that three years of sampling in our study increased our chances of collecting rare species, which resulted in the higher level of species richness.

Another reason for the high species diversity and abundance of fishes that we found in tidal creeks could be attributed to our sampling along the tidal-creek edge, which is known for its structural complexity (Montague and Wiegert, 1990) and importance as a foraging and refuge area (Baltz et al., 1993; Kneib and Wagner, 1994; Peterson and Turner, 1994). For example, Baltz et al. (1993) collected fishes in Louisiana marsh edges to look at the importance of the marsh-edge microhabitat and found that the 15 most abundant fishes were concentrated near the marsh edge and consisted mostly of early-life-history stages. They hypothesized that the fishes aggregated near the marsh edge to take advantage of the protection provided by the vegetation and the available food resources. Our sampling targeted the tidal-creek edge, and the gear we used selected for juveniles and small-adult species, which could explain the higher diversity than that seen in other studies. Another possibility is that our randomly chosen sampling sites covered a greater variety of microhabitats along tidal-creek shorelines than did the sampling of Weinstein (1979), Hettler (1989), and Peterson and Turner (1994), which could also explain the higher species richness. Despite differences in sampling methods, the collection of 80 fish species in tidal creeks appears to be unusual.

The withdrawal of fresh water from the Suwannee River would likely change the salinity regime in the Suwannee River estuary, which may in turn reduce species diversity in the region by reducing habitat availability to groups tolerant of low salinity. Furthermore, the high abundance of juvenile fishes that use low-salinity

tidal creeks as a nursery would be altered and the responses could vary on a species-specific basis (Tsou and Matheson, 2002). A decline in the amount of freshwater inflow into the tidal-creeks could lead to an overall shift towards a more saline environment and result in the expansion of seagrass habitats. However, Strawn (1961) showed that the distribution of seagrasses at Cedar Key was affected by water depth, water clarity, and the interaction of temperature and tides during winter months, making the prospect of seagrass expansion unlikely. Although a decrease in the amount of fresh water may result in an increase in water clarity through a reduction in dissolved nutrient input and reduced primary productivity, as has been seen in Apalachicola Bay, Florida (Livingston, 2003), the extreme low tides, cold temperatures, wave action, and sediment geochemistry in the Suwannee River estuary may negate the effects of increased light penetration (Koch, 2001). Therefore, a decrease in fresh water may result in an increase in high-salinity bare substrate that has been shown to be less suitable as a fish nursery than either seagrass or tidal-creek habitats (Sogard and Able, 1991; Rozas and Minello, 1998).

Tidal-creek and seagrass habitats in the Suwannee River estuary contained diverse fish communities that reflected seasonal changes associated with recruitment of YOY fishes. Many of these species are the targets of commercial and recreational activities, which support local economies. Although much of the land surrounding the Suwannee River estuary has been preserved, measures must be taken to ensure that the supply of fresh water from the Suwannee River is also preserved to maintain the integrity of the aquatic environment and the associated estuarine fish community.

Acknowledgments

We appreciate the effort of our coworkers at the Florida Marine Research Institute's Cedar Key Field Laboratory for assisting with the collection of data for this study and to Fred Vose and Cynthia Cooksey for the initial concept of this study. This paper benefitted from reviews by D. Nemeth, D. Adams, B. Winner, F. Vose, J. Whittington, K. Tisdel, R. McMichael, J. Leiby, J. Quinn, T. Tsou, and two anonymous reviewers. This project was supported in part by funding from the Department of the Interior, U. S. Fish and Wildlife Service, Federal Aid for Sport Fish Restoration Project number F-43, and Florida recreational fishing license revenues.

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Abstract—Examination of 203 adult bluefish (*Pomatomus saltatrix*) from Long Island, New York, in 2002 and 2003 and 66 from the Outer Banks, North Carolina, in 2003 revealed the presence of dracunculoid nematodes (*Philometra saltatrix*) in the ovaries of female fish. Percent prevalence reached 88% in July and then decreased after the peak of the spawning season. Bluefish contained up to 100 parasites per fish. Infection was associated with a range of disorders, including hemorrhage, inflammation, edema, prenecrotic and necrotic changes, and follicular atresia, that may prevent proper development of oocytes and probably affect bluefish fecundity. Historical occurrences, life cycle, and geographical distribution of this nematode remain largely unknown, but may play important roles in recruitment processes of bluefish.

Prevalence, intensity, and effect of a nematode (*Philometra saltatrix*) in the ovaries of bluefish (*Pomatomus saltatrix*)

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Manuscript submitted 14 July 2004 to the Scientific Editor's Office.
Manuscript approved for publication 25 July 2005 by the Scientific Editor.
Fish. Bull. 104:118–124 (2006).

Factors influencing recruitment variability in marine fishes are often complex and poorly understood. Slight variations in mortality rates, growth rates, and stage durations in the early life stages can result in tenfold or greater fluctuations in abundance (Houde, 1987). Recruitment variation appears to be driven by a combination of factors, such as environmental and oceanographic processes (Munch and Conover, 2000), diet (Friedland et al., 1988; Marks and Conover, 1993; Juanes and Conover, 1995), growth and development (McBride and Conover, 1991; Hare and Cowen, 1997) and habitat use (Able et al., 2003). The importance of parasitism and disease has, however, seldom been considered.

In the Northwest Atlantic, the bluefish (*Pomatomus saltatrix*) is distributed from Florida to the Gulf of Maine and is both commercially and recreationally important. This highly migratory species has at least two distinct spawning seasons. The first occurs in the spring, from March to May, south of Cape Hatteras, North Carolina (NC) (Kendall and Walford, 1979; Collins and Stender, 1987) and the second occurs off the coast of New York (NY) from late June to August (Norcross et al., 1974; Sherman et al., 1984), peaking in July (Chiarella and Conover, 1990). Ichthyoplankton surveys have indicated that a third spawning event occurs south of Cape Hatteras, NC, in the autumn, but juveniles spawned during this time frame have rarely been captured (Collins and Stender, 1987).

During the collection of bluefish ovaries for another study, the nematode *Philometra saltatrix* Ramachandran, 1973 was detected in the ovaries of adult bluefish. Previous studies of *Philometra* spp. in other host species have indicated that their presence can have a negative effect on fecundity (Oliva et al., 1992; Hesp et al., 2002), implying that a more complete understanding of parasites may be important to understanding reproductive success. Although factors such as female size and condition are often considered in determining reproductive success, the role of parasitism is rarely investigated (Marshall et al., 1998; Marteinsdottir and Begg, 2002). The potential effect of this nematode on the reproductive

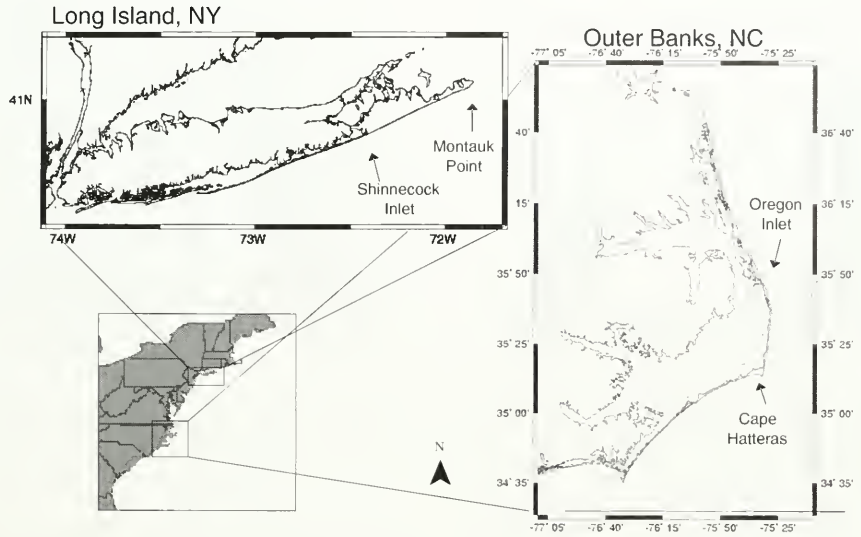

Figure 1

Map of the sampling area, Long Island, New York, and Outer Banks, North Carolina, where adult bluefish (*Pomatomus saltatrix*) were collected from commercial gill-netters, trawlers, and seafood markets in 2002–03 for examination of infestation by the nematode *Philometra saltatrix*.

potential and early life history success of bluefish is unknown. No information other than location of occurrence (Ramachandran, 1973) and a brief abstract describing the presence of philometrids in the heart of juvenile bluefish is available (Cheung et al.[1]). The purpose of this study is to investigate the prevalence, intensity, and effect of *Philometra saltatrix* in the ovaries of bluefish.

Materials and methods

Adult bluefish were collected from commercial gill-netters, trawlers, and seafood markets on Long Island, NY, and the Outer Banks, NC (Fig. 1). In NY, fish were caught off the southern coast of Long Island from Shinnecock Inlet to Montauk Point, approximately 1–15 km offshore. In NC, fish were caught approximately 1–40 km off the coast, and the majority of fish were caught 30–40 km east of Oregon Inlet.

Sampling dates were determined by the availability of fish through the local fishermen. In 2002, bluefish were sampled from mid-July through early October off the southern coast of Long Island, NY (80 females, 108 males). In 2003, fish were collected in NC in April (43 females, 21 males) and in NY from the end of June through September (123 females, 42 males).

Fork length (FL), fish weight, gonad weight, prevalence of both live and dead worms, total worm weight, and gonadosomatic indices (GSI) were recorded for each fish. Worms were often intertwined making it difficult to count the number of worms in each ovary; therefore, total worm weight per ovary was used as a proxy for intensity. Representative samples were fixed in a solution of 95% glacial acid and 5% formalin for identification. Initially, examinations of both male and female fish were conducted, but after preliminary evidence showed that nematodes were not present in the gonads of male fish, future examinations were restricted to female fish.

Haphazardly selected ovaries were preserved in 10% formalin and processed according to standard histological methods (Luna, 1968) to investigate pathologies associated with the parasite. Transverse sections were cut from the same region in the center of each ovary. These were examined under a light microscope and images were captured with a Spot Insight digital CCD and processed with ImagePro Plus software (Media Cybernetics, Silver Spring, MD).

[1] Cheung, P. J., R. F. Nigrelli, and G. D. Ruggieri. 1984. *Philometra saltatrix* infecting the heart of the 0-class bluefish, *Pomatomus saltatrix* (L.), from the New York coast. *In* S. F. Snieszko commemoration fish disease workshop, p. 27. Joint Workshop of Fish Health Section, AFS, and Midwest Disease Group, Little Rock, AR.

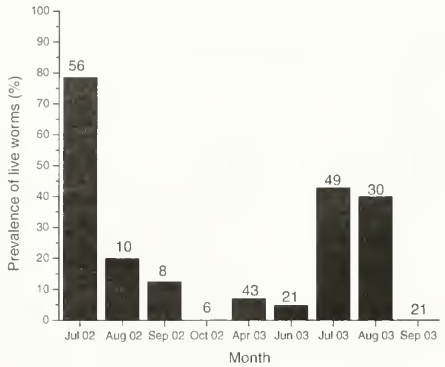

Figure 2

Monthly prevalence of live *Philometra saltatrix* in the ovaries of bluefish (*Pomatomus saltatrix*). Sample sizes are noted on the top of the bars.

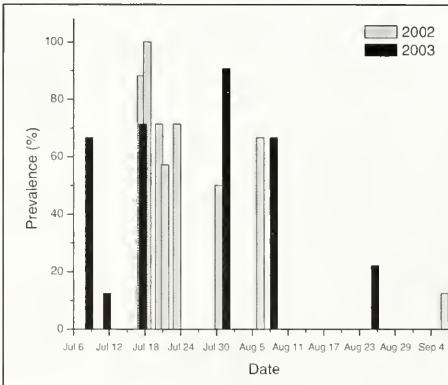

Figure 3

Daily prevalence of live *Philometra saltatrix* in the ovaries of bluefish (*Pomatomus saltatrix*) in 2002 and 2003.

Results

Description and location of worm

Philometra saltatrix was identified in the gonads of female fish ranging in size from 363 to 815 mm (FL) in both NC and NY samples. The majority of worms found in the ovaries were gravid females. Gravid female worms were visible macroscopically and most often visible even before the initiation of ovary dissection. Female worms reached a maximum of 150 mm in length and approximately 300 μm in width. Dead worms were present in all months sampled and were encapsulated by several melanised layers of fibrotic tissue. Approximately 20 juvenile male and female worms were identified in the ovary of a female fish in July 2003. These immature worms reached a maximum length of 2 mm. It should be noted, however, that not all fish were examined microscopically; therefore, it is possible that other male and juvenile worms were present in other hosts but not detected.

Prevalence and intensity

Bluefish in the western North Atlantic represent a single genetic stock (Graves et al., 1992), allowing us to combine data from New York and North Carolina to examine seasonal trends. Pooled by month of capture, the prevalence of infection varied seasonally during the two sampling years. In NC, prevalence of live nematodes was 7% in April, the spring spawning season (Fig. 2). Prevalence of live worms in NY in June was 4.8% and reached a maximum of 79% (2002) and 42% (2003) in July during the summer spawning season (Fig. 2). It is important to note that sampling in 2002 did not begin until mid-July but was conducted for the entire month in 2003. If only the second half of July is examined for both years, the prevalence is 79% and 83% for 2002 and 2003, respectively. This peak in prevalence was followed by a slow decrease in live worms until late August and early September after which time live worms were no longer detected.

Examination of prevalence by sampling day showed greater evidence of interannual variation. In the middle of July 2002, 100% of bluefish examined were infected with live *Philometra saltatrix,* whereas in 2003 the highest percentage of fish sampled that were infected was 91% (Fig. 3). Furthermore, in 2002 prevalence peaked in the middle of July, whereas in 2003 prevalence was highest at the end of the month. Additionally, live worms were detected until the end of August in 2002 but were detected two weeks later in 2003.

Intensity of parasite infection, as indicated by total live and dead worm weight per fish, reached a maximum 0.145 g (mean of 0.081 g ±0.1367) and was highest during the month of July in both years of the study (Fig. 4). Patterns of intensity were similar to those of prevalence; intensity was highest during the summer spawning season and then later decreased. One bluefish caught just south of Cape Hatteras, NC, in the beginning of May 2003 had the highest intensity observed with over 100 nematodes present (Fig. 5, A and B). This fish was not included in the data analysis because it was the only fish examined during that month, but this extreme instance of infection sets the upper bound on the level of observed intensity.

Binary logistic regression was used to test whether the presence or absence of the nematode was related to fork length (P=0.096), fish weight (P=0.292), or GSI (P=0.783), but no significant relationships were found.

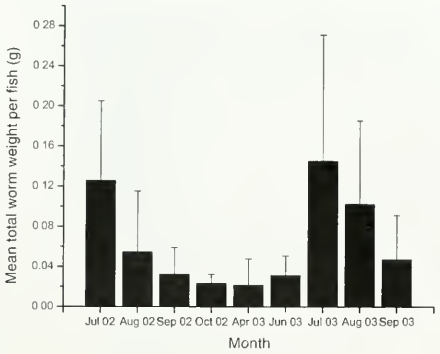

Figure 4

Monthly intensity of live and dead *Philometra saltatrix* in the ovaries of bluefish (*Pomatomus saltatrix*).

However, a significant positive correlation was found between intensity and fish weight (R= 0.169, P=0.000), intensity and fork length (R=0.221, P=0.003), and intensity and GSI (R=0.262, P=0.000). The Bonferroni method was applied to account for the multiple comparisons. Adjusted P-values are given.

Observations in adult males and YOY

Although not the target of this study, we also detected the presence of *Philometra saltatrix* in the pericardial cavity of one adult male bluefish collected in NC and three adult males in NY. Fish size ranged from 411 to 429 mm FL. Worms were not detected in the gonads of male fish.

Additionally, we detected worms in the pericardial cavity of three young of the year (YOY) bluefish caught in the Long Island Sound. Fish ranged in size from 140 to 185 FL.

Histopathology

Worms found in the ovary were surrounded by oocytes at various stages of development. The guts of these worms were most often filled with host erythrocytes. A diversity of pathological responses was noted, and significant variability was found among host individuals (Fig. 5). In many cases, infection was associated with interstitial hemorrhage in the connective tissues of the ovary. Occasionally, hemorrhage into the lumen of the ovary was also observed, but it was not clear whether this was caused by feeding activities of the worm or from tissue damage by other means. In many cases, moderate lymphocytic infiltration was observed in ovarian connective tissues. Some specimens showed marked edema in the perifollicular spaces. Prenecrotic changes, including pyknosis and cellular swelling, were observed in connective tissue cells, and necrosis of both connective tissue and oocytes (atresia) was observed in several instances. Granulomatous inflammation and fibrosis occurred in association with dead worms and, occasionally, atretic follicles. Fibrotic capsules surrounding dead worms were polylaminate and melanised and appeared to represent female worms that had expelled larvae and had subsequently died. Encapsulated worms that still contained larvae were also observed occasionally.

Discussion

Bluefish along the east coast of the United States appear to be heavily infected with the ovarian nematode *Philometra saltatrix*. Although many studies provide descriptions of various philometrid species, very few provide information about the prevalence, intensity, or effect of these nematodes. Ramachandran (1973) described the presence of several female and male worms in a single ovary but provided no information on pathological changes associated with infection.

Intensity and prevalence of *Philometra saltatrix* cycle seasonally and appear to be synchronous with the bluefish spawning cycle. Although live worms were detected from April to October, the levels of infection were higher in July than in any other month sampled and this timing is coincident with the peak of the summer spawning season off NY (Chiarella and Conover, 1990). The life cycle of *Philometra saltatrix* is unknown and, therefore, it is not clear whether initial infection coincides with the spawning season or if nematodes are acquired at an earlier time and reside in some other host tissue site before migrating to the ovaries during the spawning season, perhaps stimulated by hormonal cues from the host. Prevalence and intensity were much lower during the spring spawning season south of Cape Hatteras, NC. It is difficult to determine whether this was due to geographical differences or the limited sampling that month; it is possible that we missed the peak spawning period in 2003. The rapid decline in both prevalence and intensity after the summer spawning period indicates that *Philometra saltatrix* are released or migrate out of the host fish synchronously with the release of fish eggs. We speculate that the reproduction cycle of the nematode is closely matched to that of the host bluefish.

Other studies have reported that infection occurs after first host maturity and that female nematodes have only been observed in the gonads of females (Oliva et al., 1992; Hesp et al., 2002). Although not the focus of this study, the pericardial cavity was also found to be infected by *Philometra saltatrix* in adult males in NC and NY and in YOY bluefish in NY waters, in contradiction to these other findings. It is not clear if these YOY infections represent separate infections or if they are the same infections observed in adult females. Reviewing the reported lifecycle of other spirurid nematodes

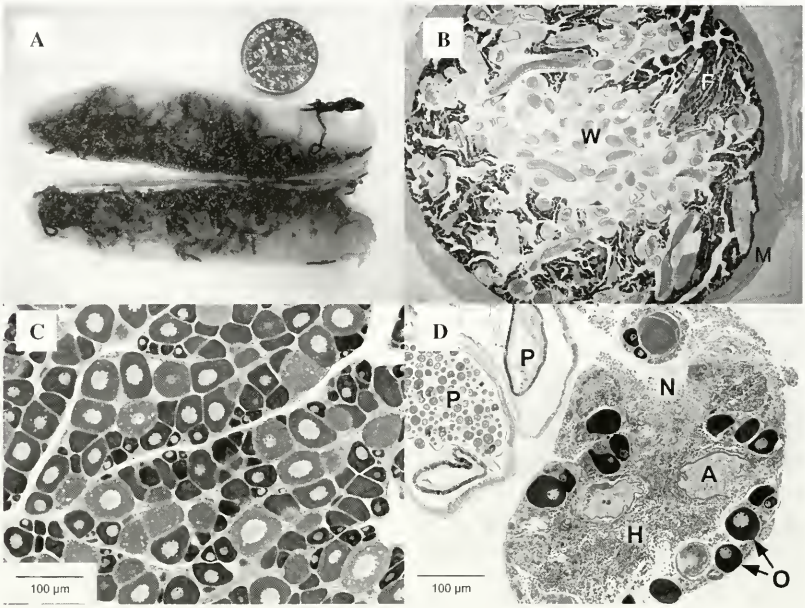

Figure 5

Observations associated with *Philometra saltatrix* infection in bluefish (*Pomatomus saltatrix*) ovaries. (**A**) Gross, bisected ovary from infected bluefish, showing heavy infection with *Philometra* (**B**) Low power view of transverse section (approximately 1.5 cm in diameter) of heavily-infected bluefish ovary. M=muscular capsule, F=ovarian follicles, W=nematodes in lumen of ovary, displacing oocytes. (**C**) Histological section of healthy ovarian tissue showing dense packing of healthy oocytes in various developmental stages, little connective tissue, and no cellular infiltrates. (**D**) Histological section of infected bluefish ovary, showing relatively fewer oocytes (O) and the presence of *Philometra* (P). In addition, there is severe interstitial hemorrhage (H) and necrosis (N) of ovarian tissue, with heavy cellular infiltration and atresia (A) of ovarian follicles.

and *Philometra* spp. (Williams and Jones, 1994), we speculate that nematode larvae are released at spawning time, pass through the copepod intermediate stage, and a second perhaps paratenic intermediate host (or perhaps pass through only one intermediate host), and infect YOY bluefish. It is important to note that most YOY bluefish larger than approximately 40 mm TL are piscivorous (Marks and Conover 1993); thus, it is possible that the infected YOY bluefish observed in this study were infected through a second intermediate host. The existence of a second intermediate fish host is supported by the observed positive relationship between host body size and parasite intensity. After initial infection, these worms reside in non-ovarian sites such as the pericardial cavity (as we observed), where they may remain quiescent until maturation of the host. At that time, worms may migrate through the tissues to the ovary for spawning and the completion of their life-cycle. This proposed life history would explain the ontogenetic and seasonal patterns of worm distribution that we observed and explain the rapid appearance of well-developed worms in the ovary at the onset of the spawning season.

The prevalence and intensity of infections we observed in bluefish were significantly higher than those reported in most other fish species. For example, intensity of infection in *Glaucosoma hebraicum* by *Philometra lateolabracis* ranged from 1 to 7 nematodes (mean of 2 nematodes) (Hesp et al., 2002), whereas prevalence of *Philometra margolisi* in the gonads of red grouper, *Epinephelus morio*, ranged from 14 to 28% depending on locality (Moravec et al., 1995) and prevalence of *Philometra lateolabracis* in *Parupeneus indicus* was 5.3% (intensity of 1–2 nematodes) (Moravec et al., 1988).

Although most studies indicate the occurrence of these nematodes to be lower than in bluefish, in a later study Moravec et al. (1997) reported prevalence of *Philometra margolisi* in the gonads of *Epinephelus morio* to be as high as 88% with an intensity of up to 84 nematodes. Additionally, although most studies report the absence of male worms (Hesp et al., 2002), we found up to 20 males in the ovary of one female fish. The high percentage of adult female bluefish that are infected may indicate that *Philometra saltatrix* are significantly affecting the reproductive success of bluefish.

Despite some studies showing deleterious effects of other parasites on fish ovaries (see for example, Adlerstein and Dorn, 1998), studies on the effects of philometrids on fish ovaries remain scarce. Indeed, in a recent review of histopathological assessments of gonadal tissue in wild fishes, Blazer (2002) made no mention of *Philometra* spp., despite the fact that it is probably the most common adult helminth observed in fish gonads. Annigeri (1962) described damage to ovaries of *Otolithus argenteus* by an unidentified philometrid, and Ramachandran (1975) mentioned necrosis in the ovaries of *Mugil cephalus* caused by *Philometra cephalus*. The infection of testes of pink snapper *Pagrus auratus* by *Philometra lateolabracis* resulted in partial or extensive atrophy of those gonads (Hine and Anderson 1981). Oliva et al. (1992) alluded briefly to lower fecundity in *Paralabrax humeralis* as a result of infection with *Philometra* but provided no data in support of this assertion. Hesp et al. (2002) studied the dynamics and effects of *P. lateolabracis* in the gonads of the Australian predatory marine fish *Glaucosoma hebraicum*, but did not observe significant pathological abnormalities associated with infection.

Histopathological changes associated with philometrid infection in bluefish were significant. The hemorrhaging, edema, inflammation, atresia, and necrosis observed most likely reduce oocyte number and quality, leading to lower fecundity. The presence of erythrocytes in the guts of nematodes indicates that the parasites were feeding on the blood of the host; this diversion of nutrients to the parasite may exacerbate the impacts of the worm on ovarian tissue. Furthermore, intense infections can reduce the effective volume of the ovary and thus lead to lower fecundity (Fig. 5, A and B).

The high prevalence, intensity, and pathological damage observed could be an important factor in recruitment variation in bluefish. Although modest interannual differences in prevalence and timing of infection were observed in this study (Fig. 4), *Philometra saltatrix* was not observed by researchers conducting studies of the GSI of bluefish from NY waters in the 1980s (Chiarella and Conover, 1990; Conover, personal observ.). Hence, it is possible that the abundance of *Philometra* may fluctuate greatly over long time scales. The reason for the current prevalence of the worm and its effect on bluefish recruitment is unknown. Future studies of this host-parasite system should seek to account for temporal variations of this kind.

Acknowledgments

We thank R. Knotoff and numerous other commercial fishermen from Shinnecock Inlet, NY, for helping us to obtain samples. B. Burns and J. Pearce of the NC Division of Marine Fisheries helped collect North Carolina bluefish. We thank R. Clarke, C. Knakal, and S. Abrams for laboratory and field assistance. We also thank two anonymous reviewers for helpful comments on the manuscript. Funding was provided by the Rutgers/NOAA Bluefish-Striped Bass Research Program and the New York State Department of Environmental Conservation.

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Duration of unassisted swimming activity for spotted dolphin (*Stenella attenuata*) calves: implications for mother-calf separation during tuna purse-seine sets

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Abstract—Size-related differences in power production and swim speed duration may contribute to the observed deficit of nursing calves in relation to lactating females killed in sets by tuna purse-seiners in the eastern tropical Pacific Ocean (ETP). Power production and swim-speed duration were estimated for northeastern spotted dolphins (*Stenella attenuata*), the species (neonate through adult) most often captured by the fishery. Power required by neonates to swim unassisted was 3.6 times that required of an adult to swim the same speed. Estimated unassisted burst speed for neonates is only about 3 m/s compared to about 6 m/s for adults. Estimated long-term sustainable speed is about 1 m/s for neonates compared to about 2.5 m/s for adults. Weight-specific power requirements decrease as dolphin calves increase in size, but power estimates for 2-year-old spotted dolphin calves are still about 40% higher than power estimates for adults, to maintain the same speed. These estimated differences between calves and adults are conservative because the calculations do not include accommodation for reduced aerobic capacity in dolphin calves compared to adults. Discrepancies in power production are probably ameliorated under normal circumstances by calves drafting next to their mothers, and by employing burst-coast or leap-burst-coast swimming, but the relatively high speeds associated with evasion behaviors during and after tuna sets likely diminish use of these energy-saving strategies by calves.

Manuscript submitted 15 February 2005 to the Scientific Editor's Office.

Manuscript approved for publication 25 July 2005 by the Scientific Editor.

Fish. Bull. 104:125–135 (2006).

Dolphin calves draft in echelon position next to their mothers for the first few weeks after birth and continue to return to drafting in echelon position frequently throughout at least their first year (Edwards[1]). "Echelon position' is the physical positioning of the calf within a few centimeters of the mother, near her mid-section, with fin motions reduced or absent (e.g., Norris and Prescott, 1961). This position takes advantage of the mother's flow field, reducing or effectively eliminating the energy cost to the calf of moving forward through the water (Weihs, 2004). Because drafting appears to be ubiquitous among dolphin calves, particularly during the neonate stage, it appears likely that drafting is an essential factor in maintaining physical association between calves and their mothers, especially when the calves are small.

In the eastern tropical Pacific Ocean (ETP) a situation occurs in which it becomes important to consider the consequences for calves of losing their drafting association with their mother. In this area, a tuna purse-seine fishery targets schools of large yellowfin tuna that associate closely with schools of dolphins, primarily the spotted dolphin (*Stenella attenuata*) (NRC, 1992). The associated schools of tunas and dolphins are located by a helicopter sent out from the purse-seine vessel and are subsequently captured through the actions of several high-powered speedboats, which are released from the purse-seiner to overtake and herd the associated animals into the closing arc of the purse-seine (NRC, 1992). Examination of the dolphins found dead in the net has revealed that 75% to 95% of the lactating females killed in the sets are not killed with an accompanying calf (Archer et al., 2004). This observed calf deficit is a potentially important factor in the lack of recovery of ETP dolphin populations despite over a decade of very low fishery mortality (Wade et al.[2]), but little is known about why or how the separation of mothers and calves occurs (Archer et al., 2004).

The chase, encirclement, and release procedure of purse-seine fishing operations tends to be relatively prolonged—chases averaging about 30 minutes, capture and confinement about 90 minutes, and postrelease swimming at least 90 minutes (Myrick and Perkins, 1995; Chivers

[1] Edwards, E. 2002. Behavioral contributions to separation and subsequent mortality of dolphin calves chased by tuna purse-seiners in the eastern tropical Pacific Ocean. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-28, 33 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

[2] Wade, P., S. Reilly, and T. Gerrodette. 2002. Assessment of the population dynamics of the northeastern offshore spotted and eastern spinner dolphin populations through 2002. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-13, 58 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

and Scott[3]). The set procedure also tends to induce relatively high, sustained swimming speeds in the dolphins. Swimming speeds of two spotted dolphins carrying velocity tags during and after tuna purse-seine sets in the ETP averaged 1.7–2.8 m/s during chase and 2.6–3.1 m/s after release, compared to undisturbed speeds of 1.2–1.9 m/s (Chivers and Scott[3]). Compared to adults, dolphin calves have smaller, less-coordinated muscles and lower aerobic capacity, especially at birth but persisting through the first year or more (Dolar et al., 1999; Dearoff et al., 2000; Noren et al., 2001; Noren et al., 2002; Eitner et al., 2003; Noren et al., 2004). Therefore, it appears possible that the observed calf deficit in the kill may result at least in part from energetics-related separation of calves from mothers during the chase or after release, as well as the inability of calves to maintain speed with adults while swimming alone.

The present study examines the possibility of energetics-related separation, by estimating the length of time (duration) during which spotted dolphin calves of different sizes ranging from neonate through two years of age can swim unassisted at various velocities. These velocity-durations are then compared to adult swimming capacities, in order to determine whether calves swimming without assistance may experience energy-based difficulty keeping up with adult dolphins during evasion from tuna purse-seine sets.

Materials and methods

Duration limits for unassisted swimming by spotted dolphin calves were calculated by combining estimates of mass-specific energy cost of steady, submerged, unassisted swimming by neonate through adult spotted dolphins, with reported swimming speed durations of adult dolphins of various species (Table 1). Swimming duration for adults was used because this information was not available for dolphin calves. The data were combined based on the assumption that the duration a given unit of dolphin muscle can sustain a given mass-specific energy cost is the same for both adults and calves within any species of dolphin. It is much more likely that swimming capacity of calves within any dolphin species is significantly lower than that of adults and that differences are particularly pronounced at birth (Dolar et al., 1999; Dearoff et al., 2000; Eitner et al., 2003; Noren et al., 2001, 2002, 2004), but the exact differences are unknown. The swimming duration estimates presented in this study therefore represent maximum durations. It is also possible that species differ in power production capacities, based on observations of blood chemistry differences between species (Ridgway and Johnston, 1965), but it is not unreasonable to assume that relative differences between species are maintained throughout the size ranges of individuals within a species, so that younger dolphins are probably less adept than adults in any particular species. Thus, although it is not yet possible to quantify differences between calf and adult swimming-duration capacities in *Stenella attenuata* in nature, they are likely greater than estimated in the present study, so that problems apparent from this study are likely greater during actual tuna purse-seine sets.

The energy cost of a steady, submerged, unassisted swimming rate was estimated in this study for velocities ranging from 1.5 to 6.0 m/s in order to encompass speeds from slow undisturbed swimming to the maximum likely to occur during attempted evasion from tuna purse-seine sets. Average velocities observed during tracking of dolphins before and after experimental sets varied from about 1.5 m/s m to about 3 m/s (Chivers and Scott[3]) but short term speeds attained during evasion maneuvers were likely to have exceeded these averages (Table 1). Total body energy costs were estimated first and then converted to mass-specific costs by dividing total estimated energy costs by the estimated total muscle weight of each size of modeled dolphin. Muscle-mass-specific measures are more appropriate than simply dividing by total body weight for comparisons between sizes because muscle fraction of body weight increases with body weight in *Stenella attenuata* in the ETP, from 35–40% in neonates to 55–60% in adults (Edwards, 1993).

Data sources

Total body energy costs were estimated for eight modeled *Stenella attenuata* ranging in size (age) from newborn through adult. Sizes were selected to emphasize changes during the early months (Table 2). Size-at-age to two years old was estimated from Hohn and Hammond (1985). Size of an adult reproductive female was estimated from Perrin and Reilly (1984). Total body wet weight, wetted surface area of body, fins, and flukes, maximum body diameter, and fraction of total body weight composed of muscle were estimated for each size of modeled dolphin by using regression equations developed from morphological measurements of ETP dolphins (Edwards 1993, Edwards[4]).

The morphological measurements were taken from 35 spotted dolphins ranging in size from 0.71 to 2.1 m total length (tip of rostrum to fluke notch). This size range encompasses all life-history stages (near-term fetus through mature adult) of the spotted dolphins found in the eastern tropical Pacific Ocean. Spotted dolphins are about 0.8 m total length at birth (Hohn and Hammond, 1985). Specimens included 22 females and 13 males (Edwards, 1993). Male specimens included

[3] Chivers, S., and M. Scott. 2002. Tagging and tracking of *Stenella* species during the 2001 Chase and Encirclement Stress Studies cruise. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-33. 23 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA. 92037.

[4] Edwards, E. 2002. Energetics consequences of chase by tuna purse-seiners for spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. National Oceanographic and Atmospheric Administration Administrative Report LJ-02-29, 32 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

three fetuses, six immature, and four mature individuals. Female specimens included three fetuses, six immature, one mature resting, one mature lactating, and 11 mature pregnant individuals. All specimens were killed during tuna fishing operations in the eastern tropical Pacific Ocean. Two of the specimens were collected in February 1980, one in July 1983, nine in July 1985, two in August 1985, seventeen in December 1985, and four were collected without a date noted (Edwards, 1993). All specimens were processed according to the same procedures prior to dissection. Immediately after the sets, the dolphin specimens were brought on board the vessel and frozen whole in the brine wells of the vessel. The specimens were transported frozen to port and then transported frozen to the Southwest Fisheries Science Center. Specimens were kept frozen until thawed in fresh water (about 27°C) just prior to dissection. Not all measurements were made on all specimens; therefore sample sizes differ between the regression equations presented below.

Energetics model The energetics model used to estimate total body cost of swimming was taken from Edwards (1992, based on Magnuson, 1978), except that 1) new data were used to estimate dolphin body parameters and 2) the estimate of fin plus induced drag was replaced by the multiplier 3 (see below). The model used standard hydrodynamic equations and methods (Hoerner, 1965; Hertel, 1969; Webb, 1975) to estimate hydrodynamic drag on a fully submerged streamlined body of revolution moving steadily in turbulent flow. Body surface area was increased to specifically include the surface area of fins and flukes (Fish[5]), and drag estimates were increased to account for body and fin movements. Because energy to move forward (thrust energy) must exactly balance the drag experienced by a steadily swimming animal, estimating total drag energy is equivalent to estimating thrust energy, i.e., the energy cost to swim (Fish and Rohr, 1999).

Model formulation Total power (P_t, in watts) required to overcome drag during steady, submerged swimming (Hertel, 1969) by a modeled dolphin of a given total length (L, rostrum to fluke notch) was estimated as

$$P_t = P_c / (E_m E_p),$$

where P_c = mechanical power (in watts) required to overcome hydrodynamic drag;
E_m = muscle efficiency; and
E_p = "propeller efficiency" (efficiency of propulsion by flukes).

E_m was assumed to be 0.2 from studies of muscle efficiencies in terrestrial animals (e.g., Goldspink 1988), man (Alexander, 1983; quoting Dickinson, 1929) and dolphins (Fish, 1993, 1996). E_p was assumed to be 0.85 based on studies by Fish (1998), Webb (1975), and Yates (1983). P_c was estimated as a function of total hydrodynamic drag (D_t, in dynes) and velocity (V, in m/s) as

$$P_m = D_t V / 10^7,$$

where the factor 10^7 converts ($D_t V$) to watts.

Total drag was estimated as a function of drag due to body, fins, and movements of body parts as

$$D_t = 0.5\rho V^2 S_w C_{d3} = 1.5\rho V^2 S_w C_d,$$

where ρ = density of seawater (1.025 g/cm^3);
S_w = wetted surface area;
C_d = coefficient of total drag; and
3 = drag augmentation factor.

S_w includes surface area of body plus fins and flukes, where estimated planar area of fins was increased by 6% to account for the curvature of the fins, based on measurements of individual slices from fins and flukes from one small and one large dolphin, 1.32 m and 1.93 m in length, respectively (Edwards, unpubl. data). Drag augmentation factor generally varies between 3 and 5 (e.g., Lighthill, 1971; Fish, 1993) and was assumed equal to the value of 3 in the present study, based on studies of gliding vs. actively swimming dolphins (Skrovan et al., 1999). The factor 3 accounts for the increase over gliding drag caused by body movements during active swimming. Use of a squared relationship between V and D_t is supported by the observed relationship between total drag and velocity in free swimming *Tursiops truncatus* (Skrovan et al. 1999, Eq. 6). Use of a cubic relationship between V and P_t is supported by observations of swimming kinematics of *Tursiops truncatus* swimming between 1 and 6 m/s (Fish, 1993).

S_w (in cm^2) was estimated as

$$S_w = 0.299 L^{2.05},$$

based on measurements from 19 *Stenella attenuata* ranging in size from 0.71 to 2.01 m, where L is total length (in cm).

C_d was estimated from the formula for drag of submerged streamlined bodies of revolution moving at constant velocity (Hoerner, 1965; Hertel, 1969; Webb, 1975) as

$$C_d = C_f \left[1 + \left(1.5(d/L)^{3/2}\right) + 7\left((d/L)^3\right)\right],$$

C_f = the coefficient of friction drag; and
d = 0.12

where d = maximum body diameter (in cm) based on measurements from 24 *Stenella attenuata* ranging in size from 0.71 to 2.01 m.

C_f was estimated from the formula for submerged streamlined bodies of revolution moving at constant velocity in turbulent flow (e.g., Webb, 1975) as

[5] Fish, F. 2002. Personal commun. Liquid Life Laboratory, West Chester Univ. Pennsylvania, West Chester, PA.

Table 1

Reported duration of various swimming speeds for several species of dolphins.

Velocity (m/s)	Duration	Publication	Species
	Burst (seconds)		
11.2	leap	Rohr et al. (2002)	*Tursiops*
11.1	2	Lang (1975)	*Stenella*
10.6	2	Lang (1975)	*Stenella*
10.3	2	Lang (1975)	*Stenella*
9.7	leap	Rohr et al. (2002)	*Tursiops*
8.8	<2	Rohr et al. (2002)	*Delphinus*
8.8	leap	Rohr et al. (2002)	*Tursiops*
8.3	7.5	Lang (1975)	*Tursiops*
8.2	<3	Rohr et al. (2002)	*Tursiops*
8.2	<120	Au et al. (1988)	*Stenella*
8.0	7.6	Lang and Norris (1966)	*Tursiops*
8.0	<3	Rohr et al. (2002)	*Delphinus*
7.8	2	Lang (1975)	*Lagenor*
7.7	2–3	Lang and Prior (1966)	*Stenella*
7.5	leap	Lang (1975)	*Tursiops*
7.4	leap	Lang (1975)	*Tursiops*
7.3	leap	Au and Weihs (1980)	*Stenella*
6.8	10	Lang and Norris (1966)	*Tursiops*
6.7	1.4	Rohr et al. (2002)	*Delphinus*
6.7	<3	Rohr et al. (2002)	*Delphinus*
6.3	10	Lang and Norris (1966)	*Tursiops*
6.4	240	Au and Weihs (1980)	*Stenella*
6.2	<2	Rohr et al. (2002)	*Tursiops*
5.9	50	Lang and Norris (1966)	*Tursiops*
6.0	2	Rohr et al. (2002)	*Delphinus*
5.6	<10	Rohr et al. (2002)	*Tursiops*
5.3	6.6	Lang and Norris (1966)	*Tursiops*
	Maximum (minutes)		
4.7	11	Au and Perryman (1982)	*Stenella*
4.4	21	Au and Perryman (1982)	*Stenella*
4.2	<8.5	Rohr et al. (2002)	*Delphinus*
	Prolonged (hours–days)		
3.5	1 hour	Au and Perryman (1982)	*Stenella*
3.2	9.3 hour	Leatherwood and L. (1979)	*Stenella*
3.1	extended period	Lang and Norris (1966)	*Tursiops*
3.1	90 min	Chivers and Scott[3]	*Stenella*
3.0	1.5 hours	Au and Perryman (1982)	*Stenella*
2.8	15 min	Chivers and Scott[3]	*Stenella*
2.6	106 min	Chivers and Scott[3]	*Stenella*
2.1	days	Chivers and Scott[3]	*Stenella*
1.9	hours	Chivers and Scott[3]	*Stenella*
1.8	hours	Chivers and Scott[3]	*Stenella*
1.7	32 min	Chivers and Scott[3]	*Stenella*
1.6	4 days	Hui (1987)	*Delphinus*
1.6	hours–days	Chivers and Scott[3]	*Stenella*
1.5	hours	Chivers and Scott[3]	*Stenella*
1.2	hours	Chivers and Scott[3]	*Stenella*
1.2	<50 hours	Perrin et al. (1979)	*Stenella*

No. of animals	Length (m)	Weight (kg)	Swimming location	Swimming condition
3			tank	maximum observed leap velocity
1	1.86	52.7	lagoon	accelerating, 25 m course
1	1.86	52.7	lagoon	accelerating, 25 m course
1	1.86	52.7	lagoon	accelerating, 25 m course
3			tank	average maximum leap velocity
1			wild	maximum observed speed
3			tank	average leap velocity
1	1.91	89	lagoon	61 m course in 300 m lagoon
6	2.6	197	small tank	maximum speed, 8 m course
300			wild	evading helicopter
1	1.91	89	lagoon	61 m course; maximum speed observed
1	1.83	105	tank	5 or 8 m course
1	2.09	91	tank	accelerating, long narrow tank
1			captive	70 m circular pool; maximum speed
1	1.91	89	ocean	swimming in speedboat waves
1	1.91	89	ocean	swimming in speedboat waves
not specified			wild	during chase by speedboats
1	1.91	89	ocean	swimming in speedboat waves
"A school"			wild	average maximum observed speed
1	1.83	105	captive	mean high swim speed
1	1.91	89	lagoon	61 m course; maximum observed speed
not specified			wild	after escaping purse seine
6	2.6	197	tank	mean high swim speed
1	1.91	89	ocean	swimming in speedboat waves
41			wild	average maximum speed evading aircraft
4			wild	maximum speed after release
1	1.91	89	ocean	swimming in speedboat waves
school no. 5			wild	maximum observed speed and duration
school no. 5			wild	swimming with ocean swells
"A school"			wild	average maximum velocity evading aircraft
school			wild	average speed evading vessel
1	2.05		wild	average speed estimated from radiotag
1	1.91	89	ocean	swimming in speedboat waves
D230			wild	postrelease velocity
school no. 2			wild	average speed evading vessel
D230			wild	velocity during chase by seiner
D19			wild	postrelease velocity
12			wild	average speed, 1992, 1993
D230			wild	average nonchase velocity, night
D230			wild	average nonchase velocity, day
D19			wild	velocity during chase by senior
2	1.76	95	tank	small, shallow round tank
2			wild	average speed, 2001
D19			wild	average nonchase velocity, day
D19			wild	average nonchase velocity, night
26			wild	minimum distance traveled, radiotag

Table 2

Dolphin model parameters. See text for formulas and rationale.

Dolphin no.	Age	Total length (cm)	Body weight (kg)	Muscle weight (kg)	Wetted surface area (cm^2)	Maximum diameter (cm)	Fineness ratio
1	new born	85	6.40	2.62	2700	13.5	6.30
2	1 week	87	6.85	2.81	2832	13.8	6.29
3	1 month	90	7.58	3.18	3036	14.3	6.28
4	3 months	98	9.76	4.29	3615	15.7	6.24
5	6 months	110	13.76	6.33	4581	17.7	6.20
6	1 year	129	22.08	11.04	6351	21.0	6.14
7	2 years	154	37.37	20.18	9131	25.4	6.07
8	adult	190	69.73	41.84	14045	31.7	5.99

$$C_f = 0.072R^{-0.2},$$

where R is Reynold's number, estimated here as

$$R = LV / v,$$

where v = kinematic viscosity (=0.01 Stokes).

The calculations above generated estimates of the power required for a whole dolphin of a given size to swim at a given velocity (P_t, in watts). Power required per kilogram of wet weight muscle (P_m), for a given velocity was estimated as

$$P_m = P_t / M_m,$$

where M_m = total *muscle* mass (wet weight in kg), estimated from total *body* mass (M_t, wet weight in kg) as

$$M_m = -2.97M_t^{0.468}$$

based on ln-ln regression of measurements from a sample of 26 *Stenella attenuata* from the ETP ranging in size from 0.71 to 2.06 m. Total muscle was used rather than some portion of measured musculature because the complex and interconnected muscle and connective tissue of dolphins makes it difficult to isolate any particular portion as uniquely responsible for locomotion (Pabst, 1990). M_t was estimated from total length (L, in cm) as

$$M_t = 0.0000119L^{2.97}$$

based on ln-ln regression of measurements from a sample of 23 *Stenella attenuata* from the ETP ranging in size from 0.71 to 2.01 m.

Results

Model corroboration

Model estimates of the cost of swimming compared reasonably well with the cost of swimming in published reports for other species of dolphins swimming 1–6 m/s, in cases where the published reports can be appropriately compared with the present model. Although a number of studies present a variety of estimates of drag, thrust power, and metabolic power at various swimming speeds for a variety of dolphins (reviewed by Fish and Rohr, 1999), comparisons of present results with many of these earlier studies would be inappropriate because either the estimates were derived from completely different models from the one used in the present study or from generally similar models but where different assumptions were made about model parameters, such as propulsive efficiency, metabolic efficiency, drag formulation, and body structure (Edwards[4]). Only appropriately comparable published results are discussed in the present study.

All weight-specific measurements in the following paragraph refer to total body mass. At estimated optimum velocities ranging from about 1.2 m/s in neonate spotted dolphins to about 1.7 m/s in adults (Edwards[4]), model estimates are approximately 3 W/kg for all sizes of spotted dolphin, compared to measurements (derived under various methods) of about 2.5–5.5 W/kg for adults of various species of dolphins, either resting or swimming about 2 m/s (Hui, 1987; Worthy et al., 1987; Williams et al., 1992; Fish, 1993; Yadzi et al., 1999). Observed average total metabolic rates calculated from oxygen consumption by two *Tursiops* (average weight 162 kg), swimming 2 and 3 m/s, were approximately 2.5 and 3.7 W/kg (Yadzi et al., 1999), compared to model estimates of approximately 2.9 and 5.9 W/kg for an adult spotted dolphin (about 70 kg) swimming at the same speeds. Model estimates of thrust power output for an adult spotted dolphin (about 70 kg) also compared well with thrust power estimated as a function of velocity from videos of five *Tursiops* swimming between 1 and 6 m/s (Fish, 1993). Given an average adult *Tursiops* weight of 230 kg, average estimated thrust power for *Tursiops* swimming 1, 3, 5, and 6 m/s was 1, 3, 14, and 23 W/kg, compared to spotted dolphin model estimates of 1, 3, 13, and 21 W/kg, respectively. These comparisons refer to mechanical power output

only, because Fish's (1993) analysis does not include metabolic efficiency. Assuming the same metabolic efficiency of 0.2 for the *Tursiops* in Fish's study as used in the present model, an estimate of total power by his *Tursiops* swimming 6 m/s is 115 W/kg (i.e., $23 \times (1/0.2)$), compared to the model estimate of about 125 W/kg for the adult spotted dolphin.

Mass-specific cost of swimming

Model estimates of mass-specific power requirements (watts per kilogram muscle, W/kg_m) for unassisted swimming by spotted dolphins in the ETP increase quickly with velocity, regardless of dolphin size, but increase much more quickly for smaller dolphins (Fig.1). Model results indicated that a neonate (85 cm) spotted dolphin must produce 3.6 times more power per kilogram of muscle than an adult swimming at the same speed. The factors are 3.5, 3.3, 2.8, 2.4, 1.8, and 1.4 times adult power for 87-, 90-, 98-, 110-, 129-, and 154-cm spotted dolphins. The factors do not vary with velocity because the relative differences between body dimensions in dolphins of different sizes remain constant regardless of swimming speed.

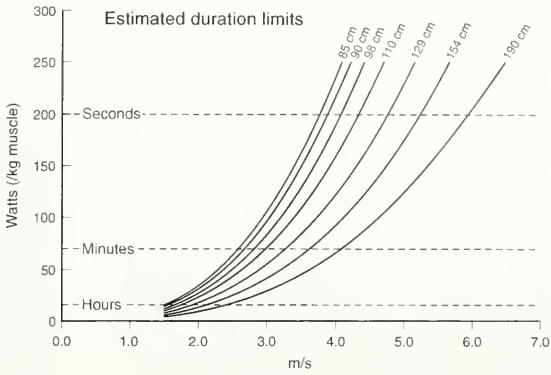

Figure 1

Estimated swimming duration limits for eastern tropical Pacific Ocean spotted dolphins (*Stenella attenuata*) of various sizes (total length, tip of rostrum to fluke notch), swimming at various speeds.

For example, at speeds typical of ETP dolphins attempting to evade speedboats during an impending tuna-purse-seine set or during escape from the net after release (about 3 m/s) (Chivers and Scott[3]), the model predicts that an 85-cm neonate swimming unassisted by its mother would require a muscle power of about 105 W/kg_m versus 30 W/kg_m for a 190-cm adult. The difference is still relatively marked even for two-year-old calves (154 cm), which would require an estimated 42 W/kg_m to maintain a steady submerged unassisted swim speed of 3 m/s, i.e., 1.4 times adult power requirements.

Velocity duration limits

Velocity duration limits for adults, drawn from literature sources, appear to range from a few seconds for burst speeds above about 5 m/s, to several minutes for maximum speeds of about 4 m/s, to hours at prolonged speeds below about 3.5 m/s (Table 1).

Estimated mass-specific muscle power required of adult spotted dolphins to achieve these speeds ranges from 208 W/kg_m for burst speeds of 6 m/s greater, to 67 W/kg_m for maximum sustainable speeds around 4 m/s, and 4–10 W/kg_m for prolonged duration speeds between 1 and 2 m/s (Fig.1).

If one assumes that these power-duration limits apply also to dolphin calf muscle, neonate dolphins (85 cm) for example, could generate a burst duration power of about 200 W/kg_m for a few seconds at unassisted swimming speeds of about 3.0 m/s, maximum duration power of about 70 W/kg_m for some minutes at about 2.2 m/s, and prolonged duration power of about 5–10 W/kg_m for hours at about 1.0 m/s (Fig.1). For two-year-old spotted dolphins (154 cm), estimated swimming duration limits were about 5 m/s for burst effort at 200 W/kg_m, about 3.5 m/s for maximum effort at 70 W/kg_m, and about 2 m/s for prolonged effort at 5–10 W/kg_m. Intermediate ages produced intermediate results.

Discussion

Model results demonstrated clearly that swimming capability of dolphin calves is much lower than that of adults. The especially pronounced difference between neonates and adults appears a likely basis for development of the ubiquitous drafting behavior observed in both captive and wild neonates. Given the large difference in swimming capacities, it is difficult to imagine how small dolphin calves could maintain any long-term association with the mother without the hydrodynamic benefits of drafting, even under normal circumstances.

During the relatively fast-paced evasion swimming associated with tuna purse-seine sets in the ETP, it appears that spotted dolphin calves swimming unassisted are likely to have serious difficulty maintaining the same speed as adults—difficulties being especially pronounced for younger dolphins. It is also likely that the differences in swimming capacity presented in this study are underestimates because they do not include effects such as positive bouyancy (Cockroft and Ross, 1990; Mann and Smuts, 1999) and soft, flexible fins and flukes that are present for several hours after birth (McBride and Kritzler, 1951; Tavolga and Essapian,

1957; Wells, 1991). Other differences persist for weeks or months, including undeveloped musculature (Eitner et al., 2003) and uncoordinated swimming and respiratory movements (Tavolga and Essapian, 1957; Taylor and Saayman, 1972; Reiss, 1984; Cockroft and Ross, 1990; Peddemors, 1990; Herzing, 1997; Mann and Smuts, 1999). Aerobic capacity is also likely to be reduced throughout the first few months, and not likely to reach adult levels until two to three years of age (Dolar et al., 1999; Dearoff et al., 2000; Noren et al., 2001, 2002, 2004). The results presented in this study also do not include the added costs of increased drag due to swimming near the surface, and repeatedly piercing it, which will occur much more often during evasion of tuna sets than during normal swimming. These other effects increase the likelihood that dolphin calves, particularly the younger individuals, will have problems coping with the swimming conditions induced during tuna purse-seine sets.

Difficulties with unassisted swimming for dolphin calves may be ameliorated to some extent by employing drafting (Weihs, 2004), burst and coast (Au and Weihs, 1980), or leap-burst-coast swimming behaviors (or a combination of these behaviors) (Weihs, 2002). Theoretically, these strategies could significantly reduce the cost to calves of moving through the water. However, it is not clear that any of these energy-saving strategies will be consistently attainable by spotted dolphin calves during herd movements associated with evading or escaping sets by tuna purse-seiners in the ETP.

Drafting can only be sustained through respiratory leaps if mother and calf leave and reenter the water with equal speed and efficiency (Weihs, 2004). Because evasion of tuna purse-seine sets involves sustained high-speed swimming characterized by repeated full-body respiratory leaps from the water (Au and Wiehs, 1980), calves are likely to tire and lose coordination more quickly than adults, and the smallest calves will be the first to experience problems. These factors may have contributed to the observed failure of a neonate dolphin calf in the ETP to successfully maintain a drafting relationship with its assumed mother during a respiratory leap while attempting to evade a vessel (Weihs, 2004).

Once the drafting relationship is disrupted, the calf appears likely to fall behind because of its physical limitations, unless its mother alters her speed so that the calf can reestablish the drafting relationship. However, review of dolphin mother-calf behavior indicates that the mother is not likely to voluntarily leave other adults during attempted evasion of tuna purse-seine sets in the ETP (Edwards[1]). Thus, the faster or longer the chase or postrelease escape period (or combination of all three factors), and the younger the calf, the more likely it appears that the calf will become separated from its mother and be left behind during periods of fast swimming by the adults. Although fast swimming for a few minutes may not pose a great problem for many calves, longer periods appear increasingly likely to lead to significant calf loss in purse-seine operations. The duration of the high-speed period is at least as important as the speed maintained during the period, given the power-duration relationship. If fast swimming is concluded quickly, it is more likely that calves could achieve the required power during the short time required. As fast-swimming persists, power capacity decreases rapidly (Fig. 1), so that more and more calves are likely to be lost because they have exceeded their ability to keep up with the adults in their school.

Even under normal circumstances, burst and coast, or burst-leap-coast, swimming patterns are not likely to provide sustained benefits to free-swimming calves until they approach adult size, coordination, and swimming capacity, because the calves will still tire more quickly than their associated adults. In the case of tuna purse-seine set evasion, sustained use of these swimming patterns may not be employed even by adults because these behaviors become less efficient as swim speed increases (Weihs, 2002). Video studies of swimming behaviors of adult *Tursiops* have shown that burst and coast periods decrease with increasing drag and cease altogether if the drag is large (Skrovan et al., 1999). In a study of dolphin gaits, an adult *Tursiops* experiencing increased drag due to an instrument pack did not use burst and coast propulsion during horizontal swimming speeds and depths at which four other adult *Tursiops* (without instrument packs) did employ short periods of burst and coast swimming. Even animals swimming without instruments at 1.5–3.7 m/s incorporated only short periods of burst and coast, and glide periods rarely exceeded 2 seconds. At the speeds characteristic of tuna purse-seine sets, dolphins tend to swim steadily or employ burst-leap-coast swimming behaviors (Weihs, 2002, Au and Weihs, 1980). With their smaller power production capacities, calves will need to shift into leap-burst-coast mode at slower speeds than will adults (Weihs, 2002), and again will tire more quickly.

A potential shortcoming of the results presented in the present study is that the model produces absolute values from single calculations, without any associated statistics or sensitivity analyses. It is more likely that a range of values for morphological, physiological and behavioral characteristics occurs within real spotted dolphin populations in the ETP, so that a range of responses is much more likely than a single response for a given size, swimming speed, and duration of chase. Lack of statistical and sensitivity analyses can be a problem where responses tend to be subtle and therefore difficult to discern. However, the model results presented in this study with respect to estimated size-related differences in power production capacities of spotted dolphins in the ETP are far from subtle, and model results are reasonably similar to energy measures derived from observations on real dolphins indicating that these model results are not unrealistic. In general, results presented here imply that older calves may be able to swim unassisted as fast and for as long as their associated adults during or after most sets (or during and after most sets) by tuna purse-seine vessels in the ETP. The markedly smaller energy production

capacities of younger calves, particularly neonates and infants, compared to adults appears to be a reasonable factor contributing to mother-calf separation during or after sets by tuna vessels in the ETP.

Management and research implications

From these observations, it appears that energetic limitations may contribute significantly to the observed calf deficit in the retrieved purse-seine by facilitating mother-calf separation during purse-seine set activity. Separation risk appears to increase strongly with decreasing calf size and with increased speed and duration of evasion-related swimming. If separation is prolonged, subsequent mortality of milk-dependent calves appears likely due to predation or starvation because adoption by a surrogate mother is unlikely in the ETP (Edwards[1]). Examination of existing aerial photographs of spotted dolphins attempting to evade helicopters and research vessels, as well as directed future experiments in which aerial observations are conducted specifically to identify and monitor mother-calf pairs over time during various chase scenarios, would be very helpful in evaluating the extent to which calf size effects predicted here occur during relatively high-speed evasion behaviors by ETP spotted dolphin schools. Estimation of the rate at which dolphins of various ages are likely to encounter tuna purse-seine sets will be another important factor in relating the results of this analysis to potential calf loss during purse-seine sets.

Assuming that power limitations are a significant factor in calf loss during evasion of tuna purse-seine sets, management strategies that could be implemented to minimize calf loss include 1) avoiding setting on schools that contain calves, particularly young calves, 2) minimizing the speed or duration of chase, and 3) minimizing the length of time dolphins are retained in the net so that mothers and calves separated during the set may reunite more quickly, if possible. Minimizing the length of time in the net is already a desired fishery goal, related to minimizing cost and the potential for dolphin mortality in the net. Minimizing chase duration is also already a desired fishery goal, because shorter chases are both less expensive and tend to be more successful. Minimizing chase speed is not a realistic goal because it would likely lead to the escape of the dolphins and the targeted tuna. Thus, the only potential improvement that might be made under current conditions (i.e., while setting on dolphin calves is permitted) would be to concentrate effort on identifying and avoiding dolphin schools with calves, presumably by scrutinizing the school from the vessel's helicopter prior to initiating a set. This may or may not be possible, depending on the ability of observers in helicopters to spot calves from the air.

Given the model results presented here, it appears that further research and perhaps management actions should be implemented to better understand and reduce the risk of separation of mothers and calves during sets by tuna purse-seiners in the ETP.

Acknowledgments

This research was conducted under Section 304 (a)(1): Stress studies, of the 1997 International Dolphin Conservation Program Act amendments to the U.S. Marine Mammal Protection Act, and subsequent Congressional directives.

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Population structure and variance effective size of red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico*

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Abstract—We assayed allelic variation at 19 nuclear-encoded microsatellites among 1622 Gulf red snapper (*Lutjanus campechanus*) sampled from the 1995 and 1997 cohorts at each of three offshore localities in the northern Gulf of Mexico (Gulf). Localities represented western, central, and eastern subregions within the northern Gulf. Number of alleles per microsatellite per sample ranged from four to 23, and gene diversity ranged from 0.170 to 0.917. Tests of conformity to Hardy-Weinberg equilibrium expectations and of genotypic equilibrium between pairs of microsatellites were generally nonsignificant following Bonferroni correction. Significant genic or genotypic heterogeneity (or both) among samples was detected at four microsatellites and over all microsatellites. Levels of divergence among samples were low ($F_{ST} \leq 0.001$). Pairwise exact tests revealed that six of seven "significant" comparisons involved temporal rather than spatial heterogeneity. Contemporaneous or variance effective size (N_{eV}) was estimated from the temporal variance in allele frequencies by using a maximum-likelihood method. Estimates of N_{eV} ranged between 1098 and >75,000 and differed significantly among localities; the N_{eV} estimate for the sample from the northcentral Gulf was >60 times as large as the estimates for the other two localities. The differences in variance effective size could reflect differences in number of individuals successfully reproducing, differences in patterns and intensity of immigration, or both, and are consistent with the hypothesis, supported by life-history data, that different "demographic stocks" of red snapper are found in the northern Gulf. Estimates of N_{eV} for red snapper in the northern Gulf were at least three orders of magnitude lower than current estimates of census size (N). The ratio of effective to census size (N_e/N) is far below that expected in an ideal population and may reflect high variance in individual reproductive success, high temporal and spatial variance in productivity among subregions or a combination of the two.

Manuscript submitted 17 July 2004 to the Scientific Editor's Office.
Manuscript approved for publication 25 July 2005 by the Scientific Editor.
Fish. Bull. 104:136–148 (2006).

Red snapper (*Lutjanus campechanus*) is a highly exploited marine fish found primarily on the continental shelf of the Gulf of Mexico (Hoese and Moore, 1977). Red snapper abundance in the northern Gulf of Mexico (hereafter, Gulf) has decreased by almost 90% in the past two decades (Goodyear and Phares[1]) owing to overexploitation by commercial and recreational fishermen, high juvenile mortality due to the shrimp-trawl fishery, and habitat change (Christman[2]; Gallaway et al., 1999). An important question for management and conservation of red snapper resources regards delineation of geographic stock structure. Should separate stocks exist, management of the fishery, including assessment and allocation, could be subdivided to avoid subregional over-exploitation and to maintain potentially adaptive genetic variation (Carvalho and Hauser, 1995; Hauser and Ward, 1998). A second important question for management is whether sufficient genetic resources exist to ensure long-term integrity of red snapper stocks. Preliminary estimates of the number of red snapper adults in the northern Gulf range from 7.8 to 11.7 million (Cowan[3]; Porch[4]), which may indicate *a priori* that sufficient genetic resources are available. However, recent studies in other, commercially exploited marine fishes have shown that genetic effective size (N_e) can be three–five orders of magnitude smaller than estimates of census size or N (Hauser et al., 2002; Turner et al., 2002). Briefly, N_e is defined as the number of individuals in an "ideal" population that would experience the same magnitude of genetic drift as the actual population (Hartl and Clark, 1989). N_e is an important biological parameter, in part because it reflects the relative effects of genetic drift and selection on nonneutral loci, and in part because it can indicate long-term risk of extinction from genetic factors (Turner et al., 2002). As long-term sustainability requires maintenance of sufficient genetic resources (Allendorf and Waples, 1996), populations (or stocks) with small N_e potentially may

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[1] Goodyear, C. P., and P. Phares. 1990. Status of red snapper stocks of the Gulf of Mexico: report for 1990, 72 p. National Marine Fisheries Service, Southeast Fisheries Centre, Miami Laboratory, CRD 89/90-05, 75 Virginia Beach Drive, Miami, FL 33149-1099.

[2] Christman, M. C. 1997. Peer review of red snapper (*Lutjanus campechanus*) research and management in the Gulf of Mexico: statistics review, 51 p. Office of Science and Technology, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 1315 East-West Highway 9th Floor F/CS, Silver Spring, MD 20910.

[3] Cowan, J. H. 2004. Personal commun. Department of Oceanography and Coastal Sciences, Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803.

[4] Porch, C. E. 2004. Personal commun. National Marine Fisheries Center, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149.

suffer reduced capacity to respond to changing or novel environmental pressures (Frankham, 1995; Higgins and Lynch, 2001).

At present, red snapper resources in the northern Gulf are managed under a single-stock hypothesis (GMFMC[5,6]). This hypothesis is supported by a number of prior genetic studies that employed allozymes (Johnson[7]), mitochondrial (mt)DNA (Gold et al., 1997; Garber et al., 2004), and microsatellites (Gold et al., 2001b). In each study, genetic homogeneity was observed across sampling localities, leading to the inference that gene flow was sufficient to maintain statistically identical allele distributions across the sampling area. All of these studies, however, either involved individuals of mixed cohorts or were based on relatively small sample sizes. Alternatively, tag-and-release and ultrasonic tracking (Fable, 1980; Szedlmayer and Shipp, 1994; Szedlmayer, 1997) have indicated that adult red snapper are sedentary and exhibit high site fidelity (but see Patterson et al., 2001). In addition, Pruett et al. (2005) used nested-clade analysis of red snapper mtDNA sequences and found evidence of different temporal episodes of both range expansion and restricted gene flow due to isolation by distance. They suggested that the spatial distribution of red snapper in the northern Gulf had a complex history that likely reflected glacial advance and retreat, habitat availability and suitability, and that the latter (i.e., physical conditions, and habitat availability and suitability) could partially restrict gene flow among present-day red snapper.

Our objectives were to more rigorously assess genetic stock structure in the northern Gulf by employing a large sample size of individuals from discrete cohorts. We report allelic variation at 19 nuclear-encoded microsatellites sampled from each of two cohorts at three different localities in the northern Gulf. Genetic homogeneity among localities was tested and contemporaneous or variance effective size (N_{eV}) at each locality was estimated from the temporal variance in allele frequencies (Waples, 1989) by using a maximum likelihood method (Wang, 2001).

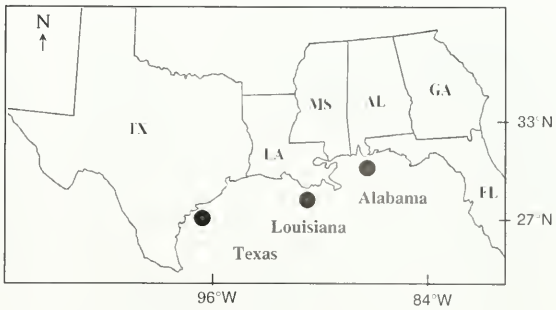

Figure 1

Sampling localities for adult red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico: northwestern Gulf (Texas), north-central Gulf (Louisiana), and northeastern Gulf (Alabama).

Materials and methods

Adult red snapper were sampled between 1999 and 2001 by angling 40–50 km offshore of Port Aransas (Texas), Port Fourchon (Louisiana), and Dauphin Island (Alabama). These localities represent western, central, and eastern subregions, respectively, within the northern Gulf (Fig. 1) but hereafter for convenience are referred to as Texas, Louisiana, and Alabama. Individual fish were aged by otolith-increment analysis (following Wilson and Nieland, 2001) and individuals belonging to the 1995 and 1997 cohorts were selected for genetic analysis. Sample sizes for the 1995 and 1997 cohorts at each locality were 203 and 211 (Texas), 286 and 272 (Louisiana), and 376 and 274 (Alabama). Tissue samples (heart and muscle) were removed from each fish and stored as described in Gold et al. (2001b). The genotype of all fish was determined at 19 microsatellites by using PCR primers and methods described in Gold et al. (2001b).

Summary statistics, including number of alleles, allelic richness (a measure of number of alleles independent of sample size), and unbiased gene diversity (expected heterozygosity) were computed for each microsatellite in each sample, with F-STAT, version 2.9.3 (Goudet, 1995). Homogeneity of allelic richness and gene diversity among samples was tested with Friedman rank tests. Departure of genotypic proportions from Hardy-Weinberg equilibrium expectations was measured within samples as Weir and Cockerham's (1984) *f*; probability of significance (P_{HW}) was assessed with a Markov-chain method (Guo and Thompson, 1992), as implemented in GENEPOP (Raymond and Rousset, 1995) and by using 5000 dememorizations, 500 batches, and 5000 iterations per batch. Genotypic disequilibrium between pairs of microsatellites within samples was tested by exact tests, as implemented in GENEPOP and by employing the same Markov-chain parameters as above. Sequential Bonferroni correction (Rice, 1989) was applied for all multiple tests performed simultaneously.

[5] GMFMC (Gulf of Mexico Fishery Management Council). 1989. Amendment number 1 to the Reef Fish Fishery Management Plan, 356 p. Gulf of Mexico Fishery Management Council, 2203 N. Lois Avenue, Suite 1100, Tampa, FL 33609.

[6] GMFMC (Gulf of Mexico Fishery Management Council). 1991. Amendment number 3 to the Reef Fish Fishery Management Plan, 17 p. Gulf of Mexico Fishery Management Council, 2203 N. Lois Avenue, Suite 1100, Tampa, FL 33609.

[7] Johnson, A. G. 1987. An investigation of the biochemical and morphometric characteristics of red snapper (*Lutjanus campechanus*) from the southern United States. Unpubl. manuscr., 26 p. National Marine Fisheries Service, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32407-7499.

Homogeneity of allele and genotype distributions among samples was examined with exact tests; significance of probability values was assessed by a Markov-chain method, as implemented in GENEPOP and using the same Markov-chain parameters as above. The degree of differentiation between pairs of samples was estimated as Weir and Cockerham's (1984) θ, as implemented in F-STAT. Sequential Bonferroni correction (Rice, 1989) was applied for all multiple tests performed simultaneously. Spatial (geographic) differences among samples was assessed from multilocus data by estimating the likelihood that any given individual could be assigned to the sample locality from which it was drawn. The Bayesian method of Rannala and Mountain (1997), as implemented in GENECLASS vers. 2.0 (Piry et al., 2005), was used to "assign" sampled individuals to a locality; the probability that an individual belonged to a given locality was calculated by using the resampling algorithm in Paetkau et al. (2004) and was based on 1000 simulated individuals. A locality was excluded as a potential origin of a given individual if the probability of the individual belonging to that locality fell below a threshold level of 0.05.

Temporal changes in allele frequencies between the two cohorts were used to estimate variance effective size (N_{eV}) at each locality. This "temporal" method (Waples, 1989) estimates effective size from the temporal variance in allele frequencies over the time interval between sampling, thus providing a contemporaneous estimate of N_e. The pseudo-maximum-likelihood method described in Wang (2001) was used to obtain estimates and 95% confidence intervals of N_{eV} by using the program MLNE available at http://www.zoo.cam.ac.uk/ioz/software.htm#MLNE. The 95% confidence intervals were obtained as the range of support associated with a drop of two logarithm units of the likelihood function, as inferred from the likelihood distribution (Wang, 2001). We used the analytical method developed by Jorde and Ryman (1995, 1996) to account for effects of overlapping generations on temporal-method estimates of N_e. In a population with overlapping generations, the magnitude of temporal allele-frequency change is dependent in part on age-specific survivorship (l_i) and birth rate (b_i). Survivorship was calculated by assuming an equal probability (S) of surviving from one year class to the next and equal probability of survival of males and females. The value of S (0.56 for Texas and 0.604 for Louisiana and Alabama) was estimated by using age-structure data of red snapper to calculate age-specific survivorship ($l_i = S^{i-1}$) for each age class i. Birth rate was estimated by calculating mean individual (wet) weight at each age class, as an indicator of relative gamete contribution. Individual weights averaged across males and females within each age class were determined by using von Bertalanffy equations (Fischer et al., 2004) for red snappers at each locality; this mean value was then multiplied by l_i to obtain the proportional contribution of each age class to offspring (p_i); p_i values were then summed over k age classes. Mean individual weights at each age class were divided by

$$\sum_{i=1}^{k} p_i$$

to produce a standardized birth rate (b_i), corrected to reflect a nongrowing population with stable age structure, i.e.,

$$\sum_{i=1}^{k} l_i b_i = 1.$$

Both age-structure and individual (wet) weight data were from the commercial and recreational catch of red snapper in the northern Gulf were provided by D. Nieland of Louisiana State University. Resulting life-history tables were used to calculate a correction factor (C) for overlapping generations by using 100 iterations of Equation 5 in Jorde and Ryman (1996). The value C can be defined as a correction term that is determined by the particular values of l_i and b_i of the population under study. G, the mean generation length in years, was calculated by using Equation 10 in Jorde and Ryman (1996). Values of C and G obtained for each locality were subsequently used to correct estimates of N_e by $N_{e\epsilon} = N_e \times [C/G]$, where N_e is the pseudo-maximum-likelihood estimate of variance effective size obtained by following Wang (2001). C and G values, respectively, for the three localities were 10.1 and 6 (Texas), 12.1 and 6.1 (Louisiana), and 10.5 and 6.8 (Alabama).

Results

Summary statistics (number of alleles, allelic richness, gene diversity; and results of tests of HW equilibrium) for each sample are given in Appendix Tables 1 and 2. Number of alleles among all samples ranged from 4 to 7 at *Prs*260 to 20–23 at *Prs*248, and averaged (±SD) 11.67 ±5.15 (1995 cohort) and 11.30 ±5.02 (1997 cohort). Allelic richness generally paralleled the number of alleles. Gene diversity among all samples ranged between 0.178–0.238 (*Lca*20) and 0.898–0.915 (*Prs*257), and averaged (±SD) 0.597 ±0.224 (1995 cohort) and 0.602 ±0.217 (1997 cohort). No significant difference in allelic richness (P=0.35) or gene diversity (P=0.07) was detected.

Four of 114 tests of conformity to Hardy-Weinberg equilibrium expectations were significant following Bonferroni correction. These included two tests in the 1995 cohort (*Prs*275 in the Texas sample and *Prs*137 in the Alabama sample) and two tests in the 1997 cohort (*Lca*22 in the Texas sample and *Prs*229 in the Louisiana sample). F_{IS} values over all loci for all four samples ranged between 0.008 and 0.029 (Appendix Tables 1 and 2). A total of 21 of 1026 (pairwise) tests of genotypic disequilibrium were significant (P<0.05) after Bonferroni correction. All 21 involved different pairs of loci (i.e., only one out of six possible tests for a given pair combination was significant) except for *Lca*64 and *Prs*328 in the 1995 cohort from Alabama and the 1997 cohort from Texas, and *Lca*64 and *Prs*248 in both cohorts sampled from Texas.

Table 1

Probability of genic and genotypic homogeneity at 19 microsatellites among spatial and temporal samples of red snapper (*Lutjanus campechanus*) sampled from the northern Gulf of Mexico. Probability values are based on exact tests; significance was assessed via a Markov-chain method (cf text). Boldface indicates significance following sequential Bonferroni correction.

Microsatellite	Genic homogeneity	Genotypic homogeneity
*Lca*20	0.018	0.031
*Lca*22	**0.001**	0.005
*Lca*43	0.044	0.065
*Lca*64	0.109	0.127
*Lca*91	**0.000**	**0.001**
*Lca*107	0.416	0.292
*Prs*55	0.179	0.212
*Prs*137	0.706	0.788
*Prs*221	0.931	0.930
*Prs*229	0.024	0.047
*Prs*240	**0.000**	**0.000**
*Prs*248	0.101	0.154
*Prs*257	0.053	0.085
*Prs*260	0.098	0.111
*Prs*275	0.819	0.893
*Prs*282	0.050	0.063
Prs 303	0.014	**0.002**
*Prs*328	0.184	0.289
*Prs*333	0.137	0.113
Overall	**0.000**	**0.000**

Significant heterogeneity (exact tests) among samples in either allele or genotype distributions (or both) was found overall and, after Bonferroni correction, at four individual microsatellites (Table 1). Pairwise comparisons (exact tests) of allele and genotype distributions between samples paralleled one another and revealed that almost all of the genetic heterogeneity was due to the 1995 cohort from Texas and the 1997 cohort from Alabama (Table 2). This result indicated that the observed genetic heterogeneity is more temporal (between cohorts) than spatial (among localities). Temporal rather than spatial heterogeneity also was indicated by the nonsignificant exact tests among localities sampled in 1997 and by the average F_{ST} values among localities (both cohorts) of less than 0.001.

Results of assignment tests are given in Table 3. On average, 53% of the individuals were "assigned" (i.e., had the highest probability of belonging) to their original locality. This proportion was significantly higher ($P<0.001$) than that expected if multilocus genotypes were distributed randomly with respect to geographic location. However, the estimated probabilities of belonging to all three localities were higher than 0.05 for 96.4–99.8% of the individuals, indicating that none of the three localities could be rejected as a potential origin. In addition, for four individuals from the Alabama sample (0.6%), all three localities were excluded as the potential origin.

The pseudo-maximum-likelihood (temporal-method) estimates of variance effective size (N_{eV}), corrected for overlapping generations, and their 95% confidence intervals for all three localities are shown in Table 4.

Table 2

Pairwise F_{ST} values (upper diagonal) and probability that $F_{ST}=0$ (lower diagonal) for twelve samples (four cohorts×three localities) of red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico. Boldface indicates significance following sequential Bonferroni correction. TX=Texas; LA=Louisiana; AL-Alabama.

	TX 95	LA 95	AL 95	TX 97	LA 97	AL 97
TX 95	—	0.0012	0.0010	0.0013	0.0010	0.0020
LA 95	**0.002**	—	0.0006	0.0007	−0.0002	0.0009
AL 95	**0.001**	0.031	—	0.0008	−0.0001	0.0015
TX 97	**0.000**	0.013	**0.001**	—	0.0005	0.0002
LA 97	0.036	0.756	0.737	0.079	—	0.0006
AL 97	**0.000**	**0.000**	**0.000**	0.045	0.073	—

Table 3

Results of assignment tests (percentage of fish assigned to a given locality) based on red snapper (*Lutjanus campechanus*) sampled from three geographic localities in the northern Gulf of Mexico. TX=Texas; LA=Louisiana; AL=Alabama.

Origin of sample (sample size)	Highest likelihood of belonging to		
	TX	LA	AL
TX (414)	53.0	24.0	22.0
LA (558)	21.0	53.0	26.0
AL (651)	21.0	26.0	53.0

Table 4

Estimates of variance effective size (N_{eV}) and 95% confidence intervals for red snapper (*Lutjanus campechanus*) sampled at three geographic localities in the northern Gulf of Mexico. Estimates were generated using the pseudo-maximum-likelihood method of Wang (2001). Values are corrected for overlapping generations, following Jorde and Ryman (1995).

Locality	N_{eV}	95% low	95% high
Texas	1098	652	2706
Louisiana	>75,000	3275	>75,000
Alabama	1235	777	2515

Estimates for the samples from Texas (N_{eV}=1098) and Alabama (N_{eV}=1235) were essentially the same, falling well within the 95% confidence intervals of one another. An exact, maximum-likelihood estimate could not be generated for the sample from Louisiana because the value of N_{eV} with highest likelihood was >75,000 and the likelihood of higher values of N_{eV} could not be computed. This estimate is more than an order of magnitude greater than the N_{eV} estimates for the other two localities and is significantly higher than those based on 95% confidence intervals.

Discussion

Genetic population structure

Results obtained from pairwise exact tests indicated that the majority of genetic differentiation detected among the twelve spatial-temporal samples of red snapper was due to allele and genotype distributions in the 1995 cohort sampled from the northwestern Gulf (Texas) and in the 1997 cohort sampled from the northeastern Gulf (Alabama). In addition, exact tests among cohorts sampled in 1997 were nonsignificant and F_{ST} values among localities (both cohorts) averaged less than 0.001. These results indicate that the genetic differences observed in the present study are temporal (between cohorts within localities) and not spatial (among localities). A "hint" of spatial differentiation was suggested by assignment tests. A total of 53% of fish were reclassified (assigned) to their original locality, a proportion that differed significantly from that expected if genotypes were distributed randomly among localities. However, for 98% of the fish, none of the three localities could be unequivocally excluded as the locality of origin.

The above results are in general agreement with other, genetics-based studies of red snapper in the northern Gulf in that little to no significant geographic heterogeneity in genetic markers, ranging from allozymes to mtDNA to microsatellites, has been detected (Johnson[7]; Gold et al., 1997; Garber et al., 2004; Gold et al., 2001b). The one exception was a study by Bortone and Chapman[8] where significant heterogeneity in both temporal and spatial restriction-fragment patterns of the mitochondrially-encoded 16S ribosomal (r)RNA gene was reported. Bortone and Chapman[8] suggested that the observed genetic heterogeneity likely stemmed from nonrandom sampling where individuals related by descent had remained in close spatial proximity to one another. In general, the "consensus" inference has been that gene flow among present-day red snapper in the northern Gulf is sufficient to offset divergence by genetic drift of the (presumed) selectively neutral genetic markers assayed. Such gene flow could involve movement of adults (Patterson et al., 2001), hydrodynamic transport of pelagic eggs and larvae (Goodyear[9]), or both.

The foregoing notwithstanding, there are a number of caveats (discussed in Pruett et al., 2005) to the inference that significant gene flow occurs among present-day red snapper in the northern Gulf. Briefly, tag-and-recapture and ultrasonic-tracking studies (Fable, 1980; Szedlmayer and Shipp, 1994; Szedlmayer, 1997) have indicated that adult red snapper are largely sedentary and nonmigratory. Significant movement of adults in the northeastern Gulf was reported by Patterson et al. (2001), but movement *per se* was mostly unidirectional (west to east) and the average distance covered in roughly a year was only ~30 kilometers. Movement of (pelagic) red snapper eggs and larvae likely occurs, but neither egg nor larval type nor length of larval life are effective predictors of gene flow in marine fishes (Shulman and Bermingham, 1995) and larval exchange rates of marine species generally appear overestimated (Cowen et al., 2000). In addition, regardless of the life-history stage at which gene flow might occur in red snapper, movement across the continental shelf should be more-or-less linear and would be expected to follow a pattern of isolation by distance where fish from proximal localities are more similar genetically than fish from more distal ones. However, the correlations between genetic and geographic distance expected from isolation by distance have not been found (Gold et al., 1997; 2001b; this article). Finally, salient differences in geologic structure, habitat structure, and ecological conditions (Rezak et al., 1985; Gallaway et al., 1998), significant differences in salinity due to freshwater outflow from river systems in the northcentral Gulf (Morey et al., 2003), and the present-day occurrence during the summer months of a major hypoxic zone that extends out along the continental shelf from the Mississippi Delta westward (Rabalais et al.[10]; Ferber, 2001) potentially could serve as barriers to movement and gene flow.

Despite these caveats, the bulk of the genetics data has indicated essentially no difference among present-day red snapper sampled across the northern Gulf. This is consistent with the unit stock hypothesis and with the inference that observed genetic homogeneity is due to substantial gene flow. However, it is important to

[8] Bortone, S. A., and R. W. Chapman. 1995. Identification of stock structure and recruitment patterns for the red snapper, *Lutjanus campechanus*, in the Gulf of Mexico. Final report for Marfin Program Grant Number NA17FF0379-03, 39 p. Southeast Regional Office, National Marine Fisheries Service, 263 13th Avenue South, Saint Petersburg, FL 33701.

[9] Goodyear, C. P. 1995. Red snapper stocks in U.S. waters of the Gulf of Mexico, 171 p. National Marine Fisheries Service, SE Fisheries Center, Miami Laboratory, CRD 95/96-05, 75 Virginia Beach Drive, Miami, FL 33149-1099.

[10] Rabalais, N. N., R. E. Turner, D. Justic, Q. Dortch, and W. J. Wiseman. 1999. Characterization of hypoxia: topic I report for the integrated assessment on hypoxia in the Gulf of Mexico. NOAA Coastal Ocean Program Decision Analysis Series No. 15, 203 p. NOAA Coastal Ocean Program, 1305 East-West Hwy., N/SCI2 SSMC4, Silver Spring, MD 20910.

note the following. First, it is possible that gene flow among present-day red snapper in the northern Gulf is limited but there has been insufficient time for semi-isolated lineages to completely sort into monophyletic assemblages. Pruett et al. (2005), on the basis of results of nested-clade analysis of mtDNA haplotypes obtained from representative samples of the same cohorts (and localities) studied in the present study, hypothesized that semi-isolated assemblages of red snapper in the northern Gulf may exist over the short term, yet over the long term comprise a larger metapopulation tied together by periodic gene flow. Similarity in allele frequencies of genetic markers (such as used here and in previous studies of red snapper) presumed to be neutral to natural selection in theory could be maintained in such a metapopulation during periods when gene flow was limited or even absent. Second, all the genetic markers studied to date are presumed to be selectively neutral and to be affected primarily by the interaction(s) between gene flow and genetic drift. Genes affecting life-history and other traits that are influenced by natural selection need not necessarily follow the same pattern(s), and geographic differences in adaptively useful alleles at such genes can be maintained even in the face of substantial gene flow (Conover et al., 2005). It is thus not implausible that red snapper across the northern Gulf could differ in allele frequency at adaptively useful genes yet be homogeneous at selectively neutral ones.

Contemporaneous effective size (N_{eV}) and present-day demographic dynamics

Estimates of contemporaneous or variance effective size (N_{eV}) for the Texas and Alabama localities (~1100) were essentially the same, but were at least an order of magnitude less than the N_{eV} estimate (>75,000) for the Louisiana locality. These estimates reflect differences in effective population size under the assumption that no immigration into a locality has occurred during the study interval, an assumption at odds with the general absence of allele-frequency heterogeneity among localities as well as the low estimates of F_{ST} between pairs of samples. Short-term immigration (within the time interval of the study) could increase the variance in allele frequencies, thus resulting in an overestimate of N_{eV} (Wang and Whitlock, 2003); whereas longer-term immigration at a (more-or-less) constant rate from a source population would have the opposite effect. The observed differences among localities could thus reflect differences in effective sizes, differences in patterns and intensity of immigration, or both. Temporal variation in allele frequencies also could occur if only a fraction of potential spawners at a locality actually contributed to recruitment and if such "temporal" subpopulations differed in allele frequencies between years. Regardless, the differences in N_{eV} may indicate that different demographic dynamics currently exist among localities.

Wang and Whitlock (2003) recently extended previous maximum-likelihood methods to allow simultaneous estimation of N_{eV} and m (rate of migration), provided data from multiple loci were available and all sources of immigrants into a focal population were known. Because of the latter, we were able to generate estimates of N_{eV} and m only for the sample from the Louisiana locality (focal population), using the samples from the Texas and Alabama localities as source populations. Surprisingly, the estimate of N_{eV} for the Louisiana sample (4887, 95% confidence intervals of 1543 and 31,254) was at least ~15 times smaller than the estimate based on no migration; m was estimated to be 0.0097 (95% confidence intervals of <0.001 and 0.0355). Clearly, more extensive sampling across the northern Gulf is warranted to obtain estimates of N_{eV} and m at other localities and to place this finding into perspective.

Effective size (N_e)/census size(N) ratios

Estimates of N_{eV} for all three sample localities were two or more orders of magnitude less than the current, preliminary estimates of adult census size (7.8–11.7 million) across the northern Gulf (Cowan[3]; Porch[4]). Given that empirically derived N_e/N ratios from a variety of vertebrates are 0.10–0.11 on average (Frankham, 1995), this result is somewhat surprising in that red snapper have a long reproductive life-span and overlapping generations (Wilson and Nieland, 2001), life-history features that are expected to increase N_e/N by limiting variance in lifetime reproductive success among individuals (Jorde and Ryman, 1995; Waite and Parker, 1996). The issue is of importance in that census sizes of many commercially exploited marine fish populations are generally orders of magnitude larger than sizes where genetic resources might be lost (Franklin, 1980; Schultz and Lynch, 1997). However, species or populations with exceedingly small N_e/N ratios potentially could be in danger of losing genetic resources, resulting in reduced adaptation and population productivity (Hauser et al., 2002). In addition, low N_e/N ratios may explain in part why there often is a poor relationship between spawning stock size and recruitment (Hauser et al., 2002). To date, N_e/N ratios smaller than 10^{-3} have been found for four other exploited marine fish species (Hauser et al., 2002; Turner et al., 2002; Hutchinson et al., 2003; Gomez-Uchida and Banks[11]).

Factors that theoretically can lower genetic effective size with respect to census size include fluctuating adult number and year-class strength (Hedgecock, 1994; Vucetich et al., 1997), and variance in reproductive success. The latter can arise from biased sex ratio, high variance in male or female reproductive success, variance in productivity among habitats, or any combination of these factors (Nunney, 1996, 1999; Whitlock and Barton, 1997). Virtually any of these factors could lower N_e/N ratios in red snapper. Biased sex-ratio, however,

[11] Gomez-Uchida, D., and M. A. Banks. 2003. Oregon State Univ., Hatfield Marine Science Center, Department of Fisheries and Wildlife, 2030 SE Marine Sci. Dr. Newport, OR 97365.

seems unlikely, because the ratio of males and females across three years of red snapper catch data was 0.97 and did not differ significantly from unity (Nieland[12]).

Variation in population number and in year-class strength, alternatively, seems likely, given the annual differences in commercial and recreational landings and the annual differences in abundance of age-0 and age-1 red snapper, respectively (Schirripa and Legault[13]). Variance in reproductive success is far more difficult to assess but can include mating systems (Nunney, 1993) that lead to differences in reproductive success between males and females, and a "sweepstakes" process (Hedgecock, 1994) where size-dependent fecundity, combined with random but family-specific early mortality (Hauser et al., 2002), leads to a large variance in the number of (surviving) offspring per parent. The latter could be effected in red snapper by nonrandom removal of related subadults or juveniles either by localized overfishing or by shrimp trawling. Finally, variance in productivity among habitats across the northern Gulf can be inferred from subregional differences in red snapper growth rates (Fischer et al., 2004) and from subregional ecological differences (Gallaway et al., 1998) that distinguish the northeastern Gulf from the northwestern Gulf. Future ecological and behavioral studies to generate estimates of variance in individual reproductive success or variation in productivity among localities are clearly warranted.

Demographic stocks

The differences in variance effective size (N_{eV}) among the geographic samples of red snapper indicate present-day differences in demographic dynamics that may include the number of individuals that produce surviving offspring, and hence by inference, census size. The factors, ecological or otherwise, promoting these demographic differences are difficult to assess but likely relate in some way to variation in food availability, habitat quality, or mortality (or a combination of all three factors). Accordingly, one might expect one or more of these factors to differ among the sample localities, given the differences in variance effective size among localities. In addition, one might expect other demographic parameters to differ as well.

Our study was part of a larger, multidisciplinary project that involved studies of age-and-growth and reproduction of red snapper at the three localities. The age-and-growth studies of Fischer et al. (2004) documented that fork length, total weight, and age-frequency distributions differed significantly among localities. Red snapper sampled at the Texas locality were significantly smaller at age and reached smaller maximum size than did red snapper sampled at the Louisiana and Alabama localities; fish sampled at the latter two localities did not differ in size-at-age or maximum size. There also was a significantly higher proportion of smaller, younger fish at the Texas locality than at the other two. The studies of reproductive capacity (Woods et al., 2003) involved only fish sampled from the Louisiana and Alabama localities but revealed that females sampled from the Alabama locality reached sexual maturity at a smaller size and younger age than did females sampled from the Louisiana locality. The differences in growth rate are likely a function in part of the more productive, nutrient-rich waters found at the Louisiana and Alabama localities and caused by the plume produced from the Mississippi River (Fischer et al., 2004), a hypothesis reinforced by the observation (Grimes, 2001) that between 70–80% of fishery landings in the northern Gulf of Mexico come from waters surrounding the Mississippi River delta. The differences in female age and size at maturity, alternatively, are thought to indicate a stressed population and to reflect a compensatory response to growth overfishing or declining population size, or a response to both (Trippel, 1995; Woods et al., 2003). Collectively, the life-history differences and the differences in genetic-based estimates of effective size strongly suggest that red snapper at the three localities represent three different, demographic stocks.

A critical issue is whether the demographic differences in life history observed among red snapper in the northern Gulf are genetic or phenotypic (environmentally induced) in origin. Most discussions of stock structure in commercially exploited marine fishes involve an explicit genetics component (Gold et al., 2001a), and typically, the absence of genetic heterogeneity within a fishery leads to management planning for a single unit stock. However, life-history traits can change rapidly in response to environmental pressures (e.g., size-selective fishing), and it has been hypothesized that the pool of genotypes that code for life-history traits is a highly dynamic property of populations, and moreover, that local adaptation(s) differentiating populations can evolve even in the presence of extensive gene flow (Conover et al., 2005). Thus, demographically different stocks could differ genetically, but not necessarily in selectively neutral markers that respond primarily to the interaction between gene flow and genetic drift. The issue also is of importance to management planning because phenotypically plastic responses due to environmental differences generally can be reversed fairly quickly, whereas genetic responses are typically much slower (Hutchings, 2004; Conover et al., 2005).

The geographic differences in red snapper in growth rates and shifts in timing of female maturity in all likelihood are due to a mix of genetic and environmental factors, as are most life-history traits in a variety of animal species, including fishes (Mousseau and Roff, 1987; Conover and Munch, 2002). A significant genetic component to growth rate is well documented in a variety of fishes under aquaculture (Dunham et al., 2001)

[12] Nieland, D. 2005. Personal commun. Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803-7503.

[13] Schirripa, M. J., and C. M. Legault. 1999. Status of the red snapper in U.S. waters of the Gulf of Mexico. Report SFD-99/00-75, 86 p. Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149-1099.

and genotypes for smaller size and younger age at maturity clearly exist (Gjerde, 1984; Tipping, 1991; Trippel, 1995). These considerations indicate that a genetic component to growth rate and age at maturity may exist in red snapper, and if so, stock-structure considerations solely on the basis of homogeneity in selectively neutral genetic markers may not be warranted.

Acknowledgments

We thank A. Fisher for providing individual age data, D. Nieland for providing life-history data, T. Turner for extensive assistance with statistical analysis, the Texas A&M supercomputing facility staff for help with parallel processing of MLNE, and S.C. Bradfield, C. Burridge, and L. Richardson for technical assistance. We also thank W. Patterson and T. Turner for helpful comments on early drafts of the manuscript, and J. Cowan and C. Porch for providing estimates of red snapper census size. Work was supported by the Gulf and South Atlantic Fisheries Development Foundation (Grant 70-04-20000/11824), by the Marfin Program of the U.S. Department of Commerce (Grant NA87-FF-0426), and by the Texas Agricultural Experiment Station (Project H-6703). This article is number 46 in the series "Genetics Studies in Marine Fishes."

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Appendix Table 1

Summary statistics at 19 nuclear-encoded microsatellite loci for the 1995 cohort of red snapper (*Lutjanus campechanus*) sampled at three localities in the northern Gulf of Mexico. n is sample size, no. of A is the number of alleles, A_R is allelic richness, H_E is gene diversity (expected heterozygosity), P_{HW} is probability of conforming to expected Hardy-Weinberg genotypic proportions, and F_{IS} is an inbreeding coefficient measured as Weir and Cockerham's (1984) f. Boldface indicates significant departures from HW equilibrium following (sequential) Bonferroni correction.

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
Lca20				*Prs240*			
n	199	286	373	n	140	276	372
No. of A	5	5	6	No. of A	20	21	23
A_R	3.39	3.37	3.00	A_R	15.84	14.94	14.96
H_E	0.170	0.215	0.172	H_E	0.917	0.901	0.885
P_{HW}	0.088	0.816	0.007	P_{HW}	0.010	0.129	0.096
F_{IS}	0.053	−0.009	0.097	F_{IS}	0.065	0.079	−0.012
Lca22				*Prs248*			
n	198	281	376	n	195	285	372
No. of A	14	17	14	No. of A	21	21	23
A_R	8.45	9.62	8.92	A_R	13.40	12.61	12.88
H_E	0.686	0.741	0.712	H_E	0.889	0.851	0.874
P_{HW}	0.176	0.317	0.013	P_{HW}	0.468	0.393	0.291
F_{IS}	0.013	0.002	0.055	F_{IS}	−0.010	0.006	0.047
Lca43				*Prs257*			
n	202	275	340	n	165	273	269
No. of A	10	11	9	No. of A	16	16	16
A_R	6.41	5.98	6.19	A_R	12.95	12.57	12.50
H_E	0.535	0.553	0.530	H_E	0.903	0.909	0.904
P_{HW}	0.585	0.763	0.669	P_{HW}	0.350	0.140	0.392
F_{IS}	−0.028	−0.006	0.017	F_{IS}	0.021	0.013	0.005
Lca64				*Prs260*			
n	197	286	377	n	189	283	376
No. of A	12	14	13	No. of A	4	5	7
A_R	7.19	7.54	6.97	A_R	3.45	3.39	3.50
H_E	0.777	0.778	0.764	H_E	0.361	0.390	0.339
P_{HW}	0.239	0.684	0.028	P_{HW}	0.507	0.285	0.185
F_{IS}	0.027	−0.025	0.014	F_{IS}	−0.011	−0.005	−0.045

continued

Appendix Table 1 (continued)

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
*Lca*91				*Prs*275			
n	201	285	375	*n*	199	286	374
No. of A	6	7	7	No. of A	9	10	9
A_R	4.49	4.16	4.43	A_R	5.46	4.91	5.25
H_E	0.608	0.559	0.580	H_E	0.635	0.595	0.590
P_{HW}	0.002	0.957	0.162	P_{HW}	**0.000**	0.604	0.183
F_{IS}	0.002	−0.066	−0.021	F_{IS}	**0.105**	−0.014	0.011
*Prs*55				*Prs*303			
n	184	277	377	*n*	200	285	374
No. of A	8	7	9	No. of A	7	13	11
A_R	3.30	3.82	3.60	A_R	5.02	5.77	5.29
H_E	0.158	0.228	0.209	H_E	0.365	0.416	0.375
P_{HW}	0.353	0.326	0.102	P_{HW}	0.785	0.559	0.007
F_{IS}	−0.030	0.001	0.073	F_{IS}	−0.029	−0.012	−0.026
*Lca*107				*Prs*282			
n	189	286	375	*n*	202	285	377
No. of A	11	12	11	No. of A	14	14	14
A_R	8.67	8.59	7.90	A_R	8.57	8.62	8.06
H_E	0.809	0.806	0.796	H_E	0.664	0.669	0.623
P_{HW}	0.871	0.451	0.776	P_{HW}	0.311	0.039	0.066
F_{IS}	0.013	0.006	−0.031	F_{IS}	−0.006	0.072	−0.035
*Prs*137				*Prs*328			
n	201	286	376	*n*	200	286	377
No. of A	13	13	17	No. of A	6	8	6
A_R	7.83	7.92	8.33	A_R	3.70	4.06	3.53
H_E	0.706	0.700	0.711	H_E	0.555	0.557	0.557
P_{HW}	0.103	0.331	**0.000**	P_{HW}	0.008	0.002	0.034
F_{IS}	0.049	0.071	**0.125**	F_{IS}	0.072	−0.086	0.020
*Prs*221				*Prs*333			
n	197	282	376	*n*	202	283	371
No. of A	16	20	19	No. of A	8	6	8
A_R	9.78	10.26	9.73	A_R	4.22	3.98	4.70
H_E	0.791	0.802	0.792	H_E	0.288	0.294	0.371
P_{HW}	0.043	0.037	0.102	P_{HW}	0.008	0.638	0.002
F_{IS}	0.018	0.050	0.053	F_{IS}	0.055	0.013	0.128
*Prs*229							
n	201	285	376				
No. of A	8	7	8				
A_R	5.96	5.44	5.39				
H_E	0.470	0.508	0.486				
P_{HW}	0.689	0.392	0.782				
F_{IS}	0.038	0.088	0.005				

Appendix Table 2

Summary statistics at 19 nuclear-encoded microsatellite loci for the 1997 cohort of red snapper (*Lutjanus campechanus*) sampled at three localities in the northern Gulf of Mexico. *n* is sample size, No. of A is number of alleles, A_R is allelic richness, H_E *is* gene diversity (expected heterozygosity), P_{HW} is probability of conforming to expected Hardy-Weinberg genotypic proportions, and F_{IS} is an inbreeding coefficient measured as Weir and Cockerham's (1984) *f*. Boldface indicates significant departures from HW equilibrium following (sequential) Bonferroni correction.

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
*Lca*20				*Prs*240			
n	211	272	269	*n*	188	234	240
No. of A	6	6	6	No. of A	20	20	22
A_R	3.72	3.35	3.78	A_R	14.22	15.37	14.34
H_E	0.238	0.184	0.206	H_E	0.897	0.898	0.885
P_{HW}	0.121	0.561	0.009	P_{HW}	0.001	0.012	0.317
F_{IS}	0.042	0.043	0.082	F_{IS}	0.092	0.043	−0.021
*Lca*22				*Prs*248			
n	208	244	266	*n*	211	271	272
No. of A	16	14	15	No. of A	21	22	21
A_R	9.88	9.36	9.45	A_R	12.58	12.91	12.67
H_E	0.769	0.757	0.771	H_E	0.872	0.867	0.882
P_{HW}	**0.000**	0.892	0.086	P_{HW}	0.176	0.616	0.334
F_{IS}	**0.106**	0.004	−0.009	F_{IS}	0.001	0.030	0.017
*Lca*43				*Prs*257			
n	210	272	272	*n*	206	266	246
No. of A	8	12	11	No. of A	17	17	18
A_R	6.22	6.48	6.19	A_R	13.24	12.86	13.51
H_E	0.587	0.536	0.528	H_E	0.908	0.898	0.915
P_{HW}	0.325	0.669	0.981	P_{HW}	0.282	0.113	0.464
F_{IS}	0.010	−0.049	−0.003	F_{IS}	0.011	0.008	0.005
*Lca*64				*Prs*260			
n	211	271	271	*n*	211	272	272
No. of A	11	13	11	No. of A	6	6	6
A_R	7.33	6.93	6.90	A_R	3.70	3.41	3.88
H_E	0.784	0.765	0.769	H_E	0.367	0.344	0.429
P_{HW}	0.086	0.749	0.495	P_{HW}	0.275	0.780	0.311
F_{IS}	0.027	0.020	0.012	F_{IS}	−0.019	0.026	−0.002
*Lca*91				*Prs*275			
n	202	268	262	*n*	211	272	273
No. of A	7	8	8	No. of A	7	9	8
A_R	4.22	4.38	4.43	A_R	5.00	5.07	4.61
H_E	0.560	0.575	0.570	H_E	0.608	0.612	0.579
P_{HW}	0.895	0.927	0.005	P_{HW}	0.711	0.334	0.441
F_{IS}	−0.070	0.039	0.030	F_{IS}	0.034	0.015	0.031
*Lca*107				*Prs*282			
n	211	264	269	*n*	211	272	273
No. of A	10	11	11	No. of A	13	12	12
A_R	7.90	8.07	8.15	A_R	8.46	8.40	7.89
H_E	0.799	0.798	0.775	H_E	0.636	0.639	0.614
P_{HW}	0.249	0.669	0.346	P_{HW}	0.886	0.556	0.141
F_{IS}	−0.104	−0.015	−0.045	F_{IS}	−0.051	0.028	0.022

continued

Appendix Table 2 (continued)

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
*Prs*55				*Prs*303			
n				*n*	211	272	270
No. of A	7	6	6	No. of A	10	9	12
A_R	4.34	3.62	3.52	A_R	5.33	5.17	6.05
H_E	0.266	0.210	0.221	H_E	0.375	0.400	0.400
P_{HW}	0.100	0.525	0.199	P_{HW}	0.527	0.344	0.781
F_{IS}	−0.017	−0.052	0.051	F_{IS}	−0.010	−0.011	−0.055
*Prs*137				*Prs*328			
n	211	272	271	*n*	211	272	273
No. of A	13	13	12	No. of A	6	6	5
A_R	7.88	7.43	8.00	A_R	3.54	3.45	3.71
H_E	0.721	0.694	0.715	H_E	0.542	0.545	0.568
P_{HW}	0.127	0.001	0.051	P_{HW}	0.323	0.108	0.191
F_{IS}	0.008	0.105	0.019	F_{IS}	0.090	−0.018	0.007
*Prs*221				*Prs*333			
n	211	271	270	*n*	211	272	272
No. of A	19	18	17	No. of A	6	7	6
A_R	10.06	9.54	10.32	A_R	3.84	4.52	4.20
H_E	0.800	0.792	0.802	H_E	0.342	0.320	0.323
P_{HW}	0.108	0.006	0.797	P_{HW}	0.571	0.819	0.412
F_{IS}	0.016	0.100	−0.025	F_{IS}	0.029	−0.022	0.032
*Prs*229							
n	211	271	269				
No. of A	7	9	9				
A_R	5.05	5.08	5.51				
H_E	0.495	0.464	0.527				
P_{HW}	0.001	**0.000**	0.020				
F_{IS}	0.081	**0.181**	0.118				

The relationship between smolt and postsmolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence

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The interaction of ocean climate and growth conditions during the postsmolt phase is emerging as the primary hypothesis to explain patterns of adult recruitment for individual stocks and stock complexes of Atlantic salmon (*Salmo salar*). Friedland et al. (1993) first reported that contrast in sea surface temperature (SST) conditions during spring appeared to be related to recruitment of the European stock complex. This hypothesis was further supported by the relationship between cohort specific patterns of recruitment for two index stocks and regional scale SST (Friedland et al., 1998). One of the index stocks, the North Esk of Scotland, was shown to have a pattern of postsmolt growth that was positively correlated with survival, indicating that growth during the postsmolt year controls survival and recruitment (Friedland et al., 2000). A similar scenario is emerging for the North American stock complex where contrast in ocean conditions during spring in the postsmolt migration corridors was associated with the recruitment pattern of the stock complex (Friedland et al., 2003a, 2003b). The accumulation of additional data on the postsmolt growth response of both stock complexes will contribute to a better understanding of the recruitment process in Atlantic salmon.

Anadromous salmonids produce cohorts of juvenile smolts that migrate over a short period of time at a nearly uniform size; however, the variability that occurs in migration timing and the size spectra of smolts is of potential interest in the study of recruitment (Hoar, 1976; Wedemeyer et al., 1980). Enhancement and restoration programs provide data on the effect of smolt size on return rate where hatchery practices both intentionally and unintentionally produce fish of varying size and quality. There are many case studies that show positive correlations between smolt size and return rate in salmonids, but nonsignificant relationships have also been observed, which underscore the fact that the contrast in size that can be achieved in hatcheries is often outside ecologically relevant limits (Farmer, 1994; Salminen et al., 1994). The functional relationship between smolt size and return rate is probably more accurately described as nonlinear and as having some optimality within the range of hatchery releases (Bilton et al., 1982; Henderson and Cass, 1991).

Researchers have also considered the effect of smolt size at ocean entry and the effect of smolt size on the ensuing growth patterns of postsmolts. Ward and Slaney (1988) described a positive relationship between return rate and smolt size for rainbow trout (*Salmo gairdneri*), suggesting that the recruitment rate of a year class was mediated by the mortality that occurred when the fish migrated to sea. When new data were added to that relationship, the original conclusions were no longer supported, indicating that factors other than smolt size at ocean entry contribute to recruitment (Ward, 2000). Although size at ocean entry may contribute to mortality risk, postsmolt growth, and the biotic and abiotic factors affecting postsmolt growth, often play a dominant role (Salminen et al., 1995). However, what has remained obscure is whether size at ocean entry influences postsmolt growth. Skilbrei (1989) and Nicieza and Branña (1993) reported negative relationships between smolt size and

Manuscript submitted 4 February 2004 to the Scientific Editor's Office.
Manuscript approved for publication 10 April 2005 by the Scientific Editor.
Fish. Bull. 104:149–155 (2006).

marine growth in Atlantic salmon, whereas Lundquist et al. (1988) and Salminen (1997) reported positive relationships. Einum et al. (2002) reported an inverse relationship between pre- and postsmolt growth of Atlantic salmon and suggested that phenotypic characteristics favoring growth in one environment may not necessarily favor growth in another. The body of mixed results sheds little light on whether smolt size confers a growth advantage to postsmolts. It also leaves in doubt the importance of freshwater experience on postsmolt survival. Common to this body of work is the dependence on samples coming from river returns and fishery catches that may not be representative of the full range of growth signatures in postsmolt populations because they do not include data from mortalities and often do not include data from some return age groups.

In this study we report on an analysis of scale growth indices from a collection of postsmolts from the Gulf of St. Lawrence. We measured freshwater growth signatures representative of smolt size and freshwater growth prior to migration and postsmolt growth was partitioned by season. These are samples of a life stage in an intermediate phase of marine life that is infrequently sampled and may be free of some of the assumed biases associated with samples from spawning fish.

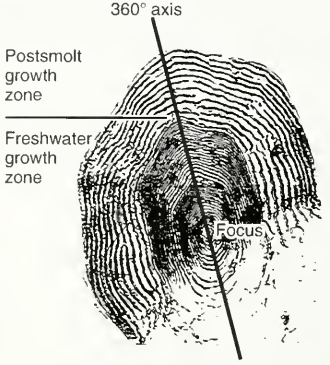

Figure 1

Postsmolt scale of Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence showing focus, freshwater growth zone, and postsmolt growth zone.

Material and methods

We collected data on scale circuli spacing that was representative of the freshwater and postsmolt growth for juvenile salmon captured in the Gulf of St. Lawrence. These postsmolt salmon were collected in 1982–84 and were originally reported in Dutil and Coutu (1988). They were captured in experimental gill nets along the northwest shore of the Gulf during the months of August to October.

Freshwater and postsmolt growth descriptors were interpreted from circuli spacing patterns deposited on the scale. Scales were cleaned and mounted between glass slides and the spacings of scale circuli were measured with a Bioscan Optimas (Media Cybernatics, Inc., Silver Spring, MD) image processing system. Freshwater zone length (FZL) was taken as the total distance from the center of the scale focus to the transition between freshwater and postsmolt growth (Fig. 1). This transition zone is defined by the appearance of the first marine intercirculus spacing, i.e., as a wider spacing (according to the reader's judgment) than the progression of spacings in the freshwater zone. The FZL ends at the last freshwater circulus. FZL was interpreted as a proxy for smolt length at migration. The mean of the last five circuli spacings during the freshwater phase was computed for each sample (CSLF, circuli spacing during last freshwater period). This circuli spacing index was interpreted as an indication of freshwater finishing growth (the final phases of freshwater growth prior to migration). Two circuli spacing indices were extracted from the postsmolt zone, the mean spacing between intercirculi 2 through 6—an interval which was interpreted as the growth index for the early marine period (CSFM, circuli spacing during first marine period)—and the mean intercirculi spacing of the next five pairs occurring later in the postsmolt growth—an interval interpreted as an index of summer growth (CSSM, circuli spacing during summer marine period). The total length of the postsmolt growth zone was also extracted (MZL, marine zone length), which was the distance from the freshwater-marine transition, starting at the last freshwater circulus to the outer edge of the scale. All measurements were made on a single scale from each specimen along the 360° axis of the scale.

We tested the functional relationship between freshwater and marine growth, early and late marine growth, and seasonal progression of the growth zones using linear regression. We tested the significance of the slope parameters for each relationship as an indication of variable dependency.

We also considered whether these data might contribute to our understanding of size selective mortality by constructing a time series plot of FZL and MZL against date of capture. An anticipated positive trend in MZL would reflect growth during the marine phase, but any trend in FZL would reflect size-specific removals attributable to size at ocean entry.

Results

Measurements were taken from the scales of 587 postsmolts collected during 1982–84. FZL averaged 0.67 mm (SD=0.163) for all samples. CSLF averaged 0.022 mm (SD=0.0049), reflecting the slower growth and more narrowly spaced circuli of the freshwater zone. The two

circuli spacing indices from the postsmolt growth zone were larger in magnitude than the index from the freshwater zone. CSFM averaged 0.061 mm (SD=0.0109) and reflected a threefold increase in circuli spacing between the freshwater and marine zones. CSSM averaged 0.064 mm (SD=0.0100), reflecting the increased growth occurring within the duration of marine residency. MZL increased over time from approximately 0.6 mm in early August to 1.2 mm by mid-October.

The data we examined to test the relationship between smolt size and freshwater finishing growth and postsmolt growth indicate an absence of any linkage between the two growth environments. We found no significant relationships between smolt sizes as represented by FZL and either spring (CSFM) or summer (CSSM) postsmolt growth as represented by the circuli spacing indices. The scatter between CSFM and FZL suggests there were no linear trends for any of the study years (Fig. 2A). None of the three regressions had slopes significantly different from zero (Table 1). There was also an absence of any relationship between CSSM and FZL as evidenced by a similar pattern of scatter for the coordinates (Fig. 2B) and by an absence of significant slopes.

The relationship was further tested by considering the growth that occurs just prior to smolt migration as an indication of smolt condition at entry into the marine environment. As was the case with the bivariate relationships with FZL, CSLF was not a significant predictor of either CSFM or CSSM (Fig. 3). None of the slopes were significantly different from zero (Table 1).

Growth in the early and later part of the postsmolt season were correlated. There were significant positive linear relationships between CSSM and CSFM for all three years (Fig. 4), indicating that the postsmolts began their marine residence with rapid growth and continued to grow at a rapid rate through summer. The slopes of all three regressions were significantly different from zero (Table 1).

A time series plot of MZL, plotted by date of capture, shows an increasing trend reflecting the growth that postsmolts experience during early marine residence (Fig. 5). For the same fish, we also plotted FZL by date of capture and found a negative trend over time, indicating that FZL decreased during the period (Table 1), which would not be consistent with selective mortality of smolts of smaller initial size.

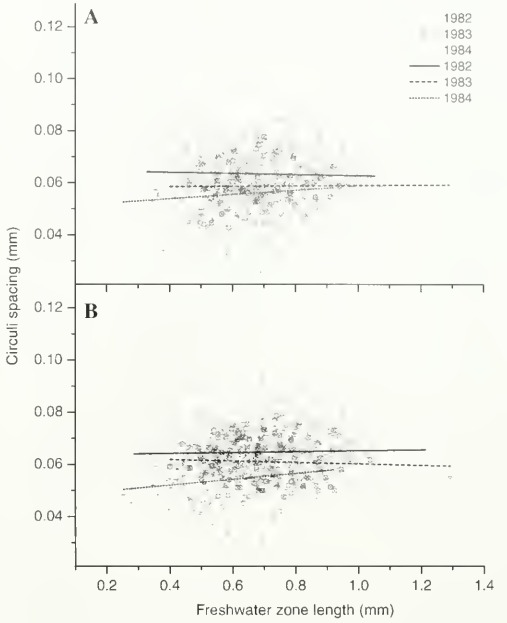

Figure 2

Relationships between circuli spacing during the early marine period (**A**) and circuli spacing during the summer marine period (**B**) and freshwater zone length for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

Table 1

Linear associations between scale growth indices and date of capture for Gulf of St. Lawrence Atlantic salmon (*Salmo salar*) postmolts. FZL=freshwater zone length; CSLF=mean of the last five freshwater intercirculi spacings; CSFM=mean spacing of intercirculi spacings 2 through 6; CSSM=mean spacing of intercirculi spacings 7 through 11; DOC=date of capture.

Linear associations		Probability H_0: slope = 0		
Predictor (X)	Dependent (Y)	1982	1983	1984
FZL	CSFM	0.53	0.87	0.57
FZL	CSSM	0.50	0.61	0.22
CSLF	CSFM	0.27	0.70	0.22
CSLF	CSSM	0.33	0.57	0.27
CSFM	CSSM	**<0.01**	**<0.01**	**<0.01**
DOC	FZL	**<0.01**		
DOC	MZL	**<0.01**		
Sample size		374	158	55

Discussion

Our main findings indicate that marine growth of postsmolt Atlantic salmon sampled from August to October in the Gulf of St. Lawrence was independent of freshwater growth history. Neither smolt size nor the last freshwater growth period of smolts prior to migration was related to postsmolt growth patterns. Furthermore,

there was no evidence that size at the smolt stage of postsmolts captured later in the season was larger than those captured earlier in the season, indicating that there was no size-selective attrition on smaller smolts during August to October. The strength of these data is that the samples were derived from collections of postsmolts, not river returns or fishery catches, and thus it is less biased and more representative of natural mortality factors. It will take considerably more data to fully test this hypothesis, but the highest priority should be given to similar sample collections, especially those collected earlier in the year (Holm et al., 2000). These data will be pivotal in interpreting the relative impact of size at ocean entry versus postsmolt growth for determing postsmolt survival.

Understanding survival during the postsmolt period is of great importance in the face of declining stock abundance and possible stock extirpations over portions of the range of Atlantic salmon (Anderson et al., 2000). With evidence showing the success of conservation efforts to increase freshwater populations (Swansburg et al., 2002), the range of potential life stages and habitats causing recruitment failure is reduced. Evidence at the population level showing coherence between early marine growth and survival at sea is still a long way from providing sufficient evidence to fully describe survival mechanisms or climate linkages. The hypothesized climate forcing appears to be related to a mismatch between ocean entry time for smolts and the thermal regime they find during their transition to marine life (Friedland et al., 2003b). The concept is supported by the growth response of postsmolts over a range of temperatures that they would likely encounter during that period of time. Atlantic salmon postsmolts follow a nonlinear growth response to temperature and optimum growth occurs at 13°C (Handeland et al., 2003). Variations in migration timing could result in fish encountering ocean conditions that are too warm or cool; these variations could explain the different associations of North American and European stocks to ocean temperatures. It would also be interesting to know if the thermal growth optimum is robust to varying feeding rations, which may be an issue for regional stock groups in the North Atlantic.

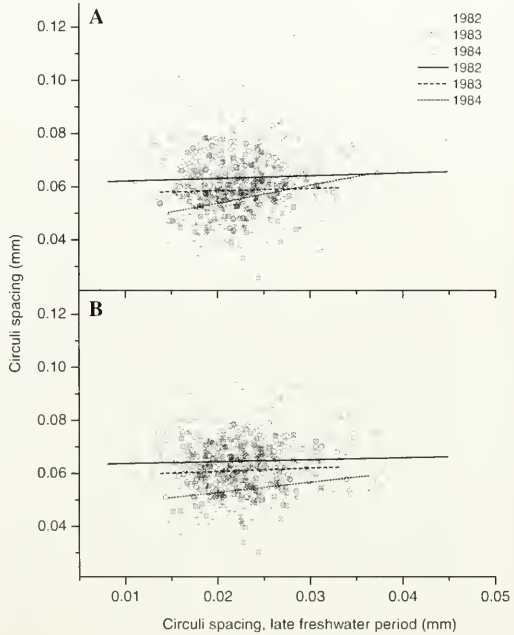

Figure 3

Relationships between circuli spacing during the early marine period (**A**) and circuli spacing during the summer marine period (**B**) and circuli spacing during the late freshwater period for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

The transition period from freshwater to marine life is characterized by a number of dynamic changes in growth and predation. The highest mortality rates for postsmolts occur during the first weeks at sea (Eriksson, 1994). As a consequence, even a minimal variation in these rates will have a large impact on adult recruitment. Size-selective mortality on juveniles has been demonstrated for other salmonids such as sockeye salmon (*Oncorhynchus nerka*) and has been shown to be seasonally concentrated (West and Larkin, 1987). Size-specific predation often occurs but predators, such as adult bird species, are not likely to grow at corresponding rates to those of the fish (Dieperink et al., 2002). Thus, size at ocean entry and the ability to grow out of the size range vulnerable to specific predators must affect the dynamics of predation rate. The period of predation vulnerability is mediated by growth rate; therefore the argument returns to what confers faster growth on postsmolts in some years?

One dynamic that challenges all stocks is the transition from predominantly invertebrate to piscivorous prey. Some authors suggest it is the success in making this transition, or the time it takes to make the transition, that dictates the amount of time the postsmolts take to grow out of the predation-vulnerable size range (Dutil and Coutu, 1988; Andreassen et al., 2001; Salminen et al., 2001). Depending on prevailing foraging conditions, this transition may be promoted by increased smolt size, as was the case in the northern Baltic Sea in 1990–93 (Salminen et al., 2001). One potential explanation for the contradictory views on the relationship between pre- and postsmolt growth in

Atlantic salmon may arise from geographical differences or year-to-year changes (or both) in prey regimes during the critical diet-transition period. In lake-run brown trout, Niva and Jokela (2000) found a positive correlation between hatchery growth rate and postsmolt growth in a lake with small fish as the main prey. In contrast, hatchery growth did not predict growth in a lake where the fish had to prey on bottom-dwelling invertebrates. This finding may indicate that assessment of individual performance may be highly specific to environments in migratory salmonids.

Size of postsmolts at ocean entry in salmonids also manifests itself in predictable patterns of life history variation. In sea trout (*Salmo trutta*) there is a close correspondence between size of juvenile stage and adult size, which is believed to have an impact on recruitment through size variation at critical life stages (Elliott, 1985). Hutchings and Jones (1998) found that smolt age and size had a small effect on the growth-rate threshold for maturity in Atlantic salmon. Smolt-size variation in sea trout has been associated with latitude, indicating that for this species recruitment strategies are likely adapted to local physical conditions, predators, and prey regimes (L' Abée-Lund et al., 1989). Wild smolts are often smaller than hatchery smolts for the same or allied strains, yet they consistently survive at higher rates (Poole et al., 2003). Obviously there are other cofactors that can explain why the wild fish overcome any advantage conferred on hatchery fish by their larger size at migration. The wild versus hatchery comparison is a relatively weak piece of evidence to use to dismiss the idea that smolt size is an important survival factor. However, a recent study of size at ocean entry in a Quebec stock of wild fish may provide more useful evidence (Dodson[1], Caron[2]). The investigators found that the size spectra of smolts were not different from the size spectra of back-calculated smolt sizes for returning adults, suggesting some factor other than size at ocean entry was controlling survival. It should be noted that postsmolts collected in the present study were of unknown origin, but the scale pattern for the freshwater zone clearly indicates that they were of wild origin.

The growth response of postsmolts may be governed by a simple response to temperature optima occurring in coastal marine waters, but it may also be more complex than that. The surface waters in the Gulf of St. Lawrence circulate in wide-scale

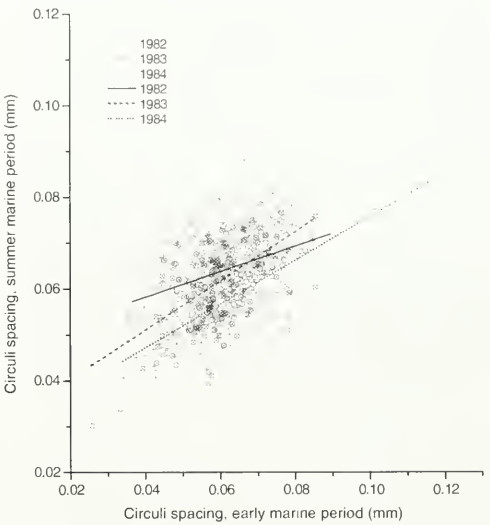

Figure 4

Relationships between circuli spacing during the summer marine period and circuli spacing during the early marine period for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

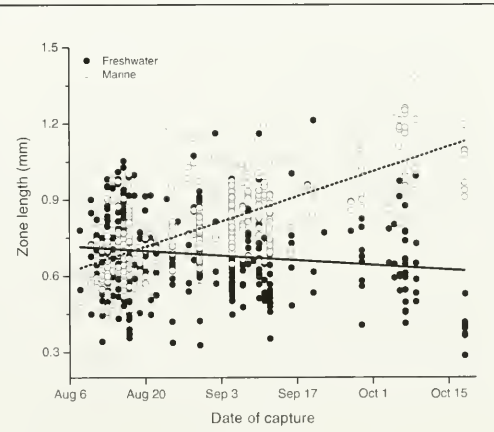

Figure 5

Freshwater zone length and marine zone length, by date of capture during the 1982 field season for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence.

[1] Dodson, J. 2004. Personal commun. Département de Biologie Pavillon Alexandre-Vachon, local 3058-B Université Laval, Québec, G1K 7P4, Canada.

[2] Caron, F. 2004. Personal commun. Direction de la Recherche Faune et Parcs Québec, 675 est, Boul. René-Lévesque Boite 92, 11e étage, Québec, G1R 5V7, Canada.

gyres over the extremely cold waters of the cold intermediate layer (CIL), thus creating a thermally complex habitat. Strong winds periodically force cold waters from the CIL to the surface (Ouellet, 1997). Postsmolts appear to be opportunistic feeders in the ocean, and despite their predominant use of surface waters, they have been known to use benthic habitats and water column features as well (Levings, 1994; Sturlaugsson, 1994). These behaviors would distribute fish in a manner independent of surface temperatures because forage behaviors are not necessarily controlled by temperature preferences. Growth in postsmolts is also affected by other physical parameters, such as photoperiod (Forsberg, 1995), and possibly by variation in sea surface salinity as shown for chum salmon (*Oncorhynchus keta*) (Morita et al., 2001). We can predict migration timing and initial migration trajectories for postsmolts, but we are hard pressed to predict the physical nature of their habitats over time and the physiological effect of these habitats on postsmolt growth.

Acknowledgments

We thank T. Sadusky for help with the initial phases of this study and two anonymous reviewers for productive comments.

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Erratum

Erratum: Fishery Bulletin 102(4): p. 568.
Calambokidis, John, Gretchen H. Steiger, David K. Ellifrit, Barry L. Troutman, and C. Edward Bowlby
Distribution and abundance of humpback whales (*Megaptera novaeangliae*) and other marine mammals off the northern Washington coast

Correction: Table 3 should read as follows

Table 3
Summary of marine mammal sightings by year during ship surveys off northern Washington. Opportunistic sightings (nontransect) are included.

Species	1995		1996		1997		1998		2000		2002		All years	
	No. of sightings	No. of animals	No. of sightings	No. of animals	No. of sightings	No. of animals	No. of sightings	No. of animals	No. of sightings	No. of animals	No. of sightings	No. of animals	No. of sightings	No. of animals
Baleen whales														
Humpback whale	25	40	54	86	23	44	27	36	24	57	79	139	232	402
Gray whale			1	1	2	3	2	3					5	7
Minke whale	3	3									1	1	4	4
Unidentified whale	4	8	3	3	11	12	1	1	3	3	4	6	26	33
Odeontocetes														
Dall's porpoise	27	72	20	64	16	43	13	46	14	48	25	133	115	406
Harbor porpoise	4	10	11	20	2	5	14	43	7	11			38	89
Pacific white-sided dolphin	4	596	16	149					4	369	4	19	28	1133
Northern right-whale dolphin									1	6			1	6
Risso's dolphin			5	57	1	5	2	11	1	6			9	79
Killer whale	3	16	2	38	2	21	2	5	3	36	2	8	14	124
Unidentified delphinid	6	9	8	56	2	4	3	5			4	18	23	92
Pinnipeds and otters														
Harbor seal	2	2	3	3	2	3	7	7	1	1			15	16
Elephant seal	6	6	10	10	2	2			2	2			20	20
California sea lion							1	1	3	3			4	4
Steller sea lion							3	5	1	1			4	6
Northern fur seal	6	6	5	5	1	2	9	9	1	1	6	6	28	29
Sea otter							3	3					3	3
Unidentified pinniped	4	4	3	3	1	2	4	4	1	1			13	14
Total sightings	94	772	141	495	65	146	91	179	66	545	125	330	582	2467

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Volume 104
Number 2
April 2006

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Number 2
April 2006

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Abstract—Blacktail comber (*Serranus atricauda* Gunther) is a commercially important species in the Canary Islands fisheries. A total of 425 individuals were collected and histological techniques were used to investigate the reproductive data. Results indicated that the spawning season occurred throughout the year, peaking between March and July. Individuals reached 50% maturity at 19.3 cm TL and 95% at 33.1 cm TL. Batch fecundity estimates ranged from 21,774 to 369,578 oocytes per spawning event for specimens from 22.2 to 39.8 cm TL. Blacktail comber was estimated to spawn 42 times/year and 26.5% of individuals spawned, on average, every 3.8 days. Estimates of potential annual fecundity for the species ranged from 0.91 to 15.5 million oocytes, and an average of 5.1 ±4.1 million.

Spawning season, maturity sizes, and fecundity in blacktail comber (*Serranus atricauda*) (Serranidae) from the eastern-central Atlantic

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Manuscript submitted 20 November 2003 to the Scientific Editor's Office.
Manuscript approved for publication 23 June 2005 by the Scientific Editor.
Fish. Bull. 104:159–166 (2006).

Fish of the genus *Serranus* are synchronous hermaphrodites; male and female tissues are simultaneously functional (Smith, 1965). The most common style of reproduction is serial monogamy, in which individuals are solitary during the day before pairing up and spawning in the late afternoon (Fischer, 1986). During spawning one fish in each pair functions as a male and the other as a female and cross-fertilization occurs. This special characteristic, and the possibility of self-fertilization, have encouraged detailed studies of the gonad structure of the genus *Serranus* (Atz, 1965; Fishelson, 1970; Reinboth, 1970; Febvre et al., 1975; Zanuy, 1977; Bruslé, 1983; Abd-el-Aziz and Ramadan, 1990; García-Díaz et al., 1997, 2002), although knowledge of other reproductive features is scarce.

Models of dynamic population used in the management of fishery resources and in biological studies of fish require knowledge of the reproductive system (Koslow et al., 1995). This includes gonad morphology (external and cellular description of the ovary and testis), reproductive pattern (hermaphoditism or gonocorism), reproductive behavior, reproductive cycle, spawning season duration, size at maturity, sex ratio, size at sexual transition, and fecundity. Of all these reproductive features, fecundity is the most difficult biological parameter to obtain, although it is of interest to fishery scientists both as a critical parameter for stock assessments based on egg production methods and as a basic aspect of fish biology and population dynamics. To calculate fecundity, fish are divided into determinate and indeterminate spawners (Hunter and Macewicz, 1985a; Hunter et al., 1992). With indeterminate spawners, multiple or serial batches are noted, and spawning may take place many times during a protracted spawning

season. Therefore fecundity is very difficult to determine before the onset of the spawning season because 1) there is no way to differentiate between the oocytes that are going to be shed during the next season from those which will remain for future seasons, and 2) the number of reserve oocytes that will mature during the next spawning season cannot be predetermined (Hunter and Goldberg, 1980; Hunter et al., 1985). To estimate indeterminate annual fecundity, the mean number of eggs per batch and spawning frequency throughout the spawning season must be calculated. Owing to the complexity of obtaining these data, fecundity studies are normally limited to determinate spawners or pelagic species of substantial economical interest (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985a; Karlou-Riga and Economidis, 1997; Murua et al., 1998).

The blacktail comber (*Serranus atricauda* Günther, 1874), is a littoral (3–150 m) benthic species, ranging throughout the eastern central Atlantic (from the Bay of Biscay to Mauritania, the Azores, Madeira, and the Canary Islands) and in the western Mediterranean. It is, therefore, a species of wide distribution and commercial interest in many regions (Bauchot, 1987; Smith, 1990). In the Canary Islands, it is an economically important species for small-scale inshore fisheries (Pérez-Barroso et al., 1993). García-Díaz et al. (1999, 2002) determined that this species is a functional simultaneous hermaphrodite. The ovary is classified as asynchronous, i.e., various stages of oocyte development occur simultaneously (primary growth stage, yolk vesicle formation, vitellogenesis, oocyte maturation, and mature egg). The histological structure of the gonad and of the sperm indicates that this species is an externally fertilizing teleost.

The objective of this article is to increase our understanding of the reproductive biology of the blacktail comber in the Canary Islands by estimating its spawning season duration, size at maturity, and fecundity.

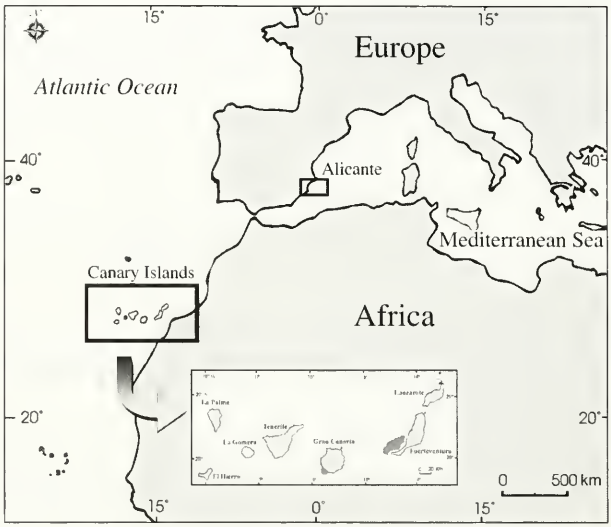

Figure 1

Location of sampling areas (shown with dark shading) for blacktail comber (*Serranus atricauda*) specimens from the Canary Islands (eastern-central Atlantic).

Materials and methods

Sampling

A total of 425 individuals of *S. atricauda*, ranging from 15.7 to 43.2 cm total length were sampled monthly from commercial catches off the Canary Islands between September 1992 and November 1994 (Fig. 1).

Total length (TL), to the nearest centimeter, was measured for each specimen, together with the total and gutted weight (TW and GW, respectively), gonad weight (GNW), and liver weight (LW), with an accuracy of 0.1 g. Gonads were removed and fixed in 10% buffered formaldehyde. After 24–48 h, they were dehydrated, embedded in paraffin wax, sectioned in longitudinal or cross-sections (4 to 5 μm thick), and stained with Harris "hematoxylin-Puttis" eosin. Oocyte stages and spermatogenic cells were classified according to García-Díaz et al. (2002). Postovulatory follicles and atresia were also characterized according to the criteria used for *Engraulis mordax* by Hunter and Goldberg (1980) and Hunter and Macewicz (1985b). Maturity stages (MS) were determined from histological observations (the development of the ovary and testis and also the presence and absence of different types of the oocytes and spermatocytes) according to García-Díaz et al. (1997, 2002) (Table 1). The developmental stages of the oocytes were categorized according to Selman et al. (1993): primary growth (stage I); cortical alveoli formation (stage II); vitellogenesis (stage III); oocyte maturation (stage IV); and mature egg (stage V).

Seasonality of gonad development

Monthly changes in the five following variables were analyzed to determine the spawning season of blacktail comber (García-Díaz et al., 1997):

1 Percent frequency of the maturity stages; this indicates population changes in gonad development.
2 Gonadosomatic index ($GSI=(gonad\ weight/gutted\ weight)\times 100$): this shows differences in development of the gonads with respect to gutted body weight;

Table 1
Description of gonad stages according to García-Díaz et al. (1997, 2002).

Maturity stage	Histological appearance
I. Immature	Ovary contains oogonia and oocytes from primary growth (stage I). Testis formed mainly by spermatogonia and primary spermatocytes. Ovary and testis joined by connective tissue.
II. Developing virgin, or recovering-spent	Ovary begins to acquire ovarian lamellae. Contains stage-I oocytes and yolk-vesicle-formation-stage oocytes (stage II) in advanced phases. Testis arranged in tubules with spermatogonia and primary and secondary spermatocytes.
III. Developing, maturing	Ovary with oocytes at all previous stages and oocytes in vitellogenic stage (stage III). Seminiferous tubules contain all spermatogenic cells.
IV. Ripe	Ovary with oocytes at all previous stages and with maturation oocytes (stage IV), mature and hydrated eggs (stage V). Atresic oocytes and postovulatory follicles appear. Testis completely mature, tubules filled with spermatozoa (which accumulate in deferent duct next to gonadal wall) to be expelled.
V. Spent	Oocytes undergoing regression and reabsorption. Numerous atresic oocytes. Testis in regression; cells appear fused, form semicontinuous mass.

3 Hepatosomatic index ($HSI=(liver\ weight/gutted\ weight)\times 100$): this estimates the relative size of the liver to body weight:
4 Condition factor ($Kn=(total\ weight/\ TL^b)\times 1000$): this is as an overall measurement of robustness of the fish, b being the exponential of the regression $TW = aTL^b$, which is 3.25 according to Tuset et al. (2004);
5 Oocyte diameter (DO): this gives information on the cell development of each individual. To obtain this value, of ten fish randomly chosen from the monthly samples, the diameters of the first 50 oocytes encountered were measured with an ocular micrometer. Measurements were taken only of oocytes sectioned through the nucleus.

Length at sexual maturity

Total length of all individuals was used to estimate the size at first maturity and size at mass maturity. These are defined as the sizes (TL) at which 50% ($TL_{50\%}$) and 95% ($TL_{95\%}$) of all fish sampled are at the relevant maturity stage (developing MS III, ripe MS IV, or spent MS V) (García-Díaz et al., 1997). The proportions were estimated at length classes of 1 cm, and the data were fitted to the logistic curve (Pope et al., 1983):

$$p = 100/(1+\exp(a+bTL)),$$

where p = percentage of mature individuals as a function of size class (TL); and
a and b = specific parameters that can change during the life cycle.

A logarithmic transformation was applied to the equation to calculate the parameters a and b by means of linear regression.

Reproductive potential

The pattern of annual fecundity (indeterminate or determinate) was assessed by oocyte size-frequency distribution (Hunter and Macewicz, 1985a). Ten fish ranging between 18.1 and 31.5 cm TL in ripe stage were selected for analysis of oocyte size-frequency distribution—five fish in March and another five in July—to represent early and late gonad development (White et al., 2003). Because the mean size (t-test, $P>0.05$) was not significantly different between both samples, one frequency distribution was obtained for each month. The diameters of the first 500 oocytes encountered were measured with an ocular micrometer for each fish. Measurements were taken only of oocytes sectioned through the nucleus.

Gonads of individuals in MS III (developing) and MS IV (ripe) were collected to estimate fecundity. One lobule was fixed in 10% buffered formaldehyde (24 h) for histological study, and the other was weighed and preserved in Gilson's fluid to estimate fecundity. Gonads with postovulatory follicles were omitted from batch fecundity estimates (Hunter et al., 1985).

The oocyte size-frequency method was applied to determine the batch fecundity (Hunter et al., 1985). This entails counting the number of oocytes in the most developed modal group of oocytes and plotting the size-frequency. In each lobule 200 oocytes were measured with the Nikon digital counter SC-112 and data processor DP-201 connected to the micrometer stage of a profile projector (V-12A, Nikon, Melville, NY). The routine NORMSEP (normal distribution separator) of FAO-ICLARM Stock Assessment Tools (FISAT II, vers. 1.0.0, FAO, Rome, Italy) program was used to separate the most developed modal group of oocytes based on Hasselblad's maximum likelihood method (Hasselblad, 1966).

Batch fecundity was estimated gravimetrically by using the oocyte size-frequency method (Hunter et

al., 1985; Yoneda et al., 2001). Samples were filtered through a 100-mm mesh sieve (approximately the minimum diameter of vitellogenic oocytes, García-Díaz et al., 2002) and were carefully washed under running distilled water to eliminate tissue remains and fixer. We used a sieve made from a piece of nylon plankton net inserted between two sections of PVC pipe, 15 cm in diameter and 10 cm in depth (Lowerre-Barbieri and Barbieri, 1993). A compact mass of oocytes was dried for 24 hours on filter paper and weighed precisely to 0.001 g. Afterwards, a subsample of 0.2 g was selected and placed in the count dish, covered with 3–4 drops of glycerin, and the number of oocytes in the sample was tallied with a hand counter. Batch fecundity was considered to be the total number of oocytes within the most developed modal group of oocytes (Hunter et al., 1985).

Spawning frequency (the number of spawnings per year by an individual) was estimated by dividing the duration of the spawning season by the average number of days between spawning for all individuals (Hunter and Macewicz, 1985a). The duration of the spawning season was the number of days between the first (7^{th} February) and last (16^{th} July) occurrence of hydrated oocyte or postovulatory follicles. The average number of days between spawning was the inverse of the percent frequency of hydrated individuals, multiplied by 100 (Collins et al., 1998).

The potential annual fecundity estimates (PAFEs) were obtained by multiplying batch fecundity by spawning frequency, and relative fecundity was defined as PAFE divided by individual weight (Hunter et al., 1992). The relationships between PAFE and TL, PAFE and TW, and PAFE and gonad weight (GW) were calculated by the following compound equation:

$$PAFE = a\ (b^X),$$

where X = TL, TW, or GW; and
a and b = specific parameters.

A logarithmic transformation was applied to the equation to calculate parameters a and b by using linear regression (Zar, 1996).

Results

Spawning season and maturity sizes

The specimens revealed the presence of maturing and ripe individuals between December and October, excluding January because only one individual was sampled then. This finding may indicate that the population spawns throughout this period, peaking between February (37.5%) and June (89.8%) (Fig. 2).

The highest values for GSI (Fig. 3A) occurred between March (2.06) and July (3.37) and a peak of maximum activity occurred in June (3.93), decreasing over the following months. The HSI (Fig. 3B) and Kn (Fig. 3C) presented irregular values during the annual cycle. Consequently, no correlation was observed between either ovarian and liver growth with ovarian and fish growth. Oocyte diameter (DO) (Fig. 3D) values varied similarly to those from the GSI; highest values occurred from March (261.37 μm) to July (275.07 μm) and peaked in June (365.85 μm). However, the variability of oocyte diameter showed the presence of mature individuals (MS III + IV) in the months of September, October, and December, according to gonad classification.

The smallest individual with mature gonads was 16 cm TL. The maturity curve established a $TL_{50\%}$ of 19.3 cm and $TL_{95\%}$ of 33.1 cm (Fig. 4).

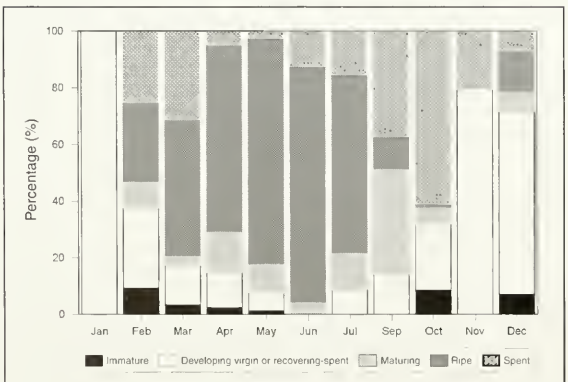

Figure 2

Monthly variation (%) in the maturity stages in the blacktail comber (*Serranus atricauda*).

Reproductive potential

From the oocyte size-frequency distributions, we concluded that the type of fecundity in this species is indeterminate evidenced by the lack of hiatus between advanced yolked oocytes and less mature oocytes (Fig. 5).

Batch fecundity estimates (n=28) varied between 21,774 and 369,578 oocytes. These estimates came from blacktail comber ranging in total length from 22.2 to 39.8 cm, total weight from 127.2 to 896.6 g, gutted weight from 122.9 to 834.6 g, and gonadal weight from 1.3 to 41.3 g.

The spawning-frequency estimate for individuals from 17.2 to 43.2 cm TL was 42 times/year, and 26.5% (45/170) of individuals spawned at an average of every 3.8 days.

Potential annual fecundity estimates ranged from 0.91 to 15.5 million oocytes, and an average of 5.1 ±4.1 million (Fig. 6). Relative fecundity varied between 5062 and 20,869 oocytes per gram of individual, and mean relative fecundity was 10,547 ±4148 oocytes.

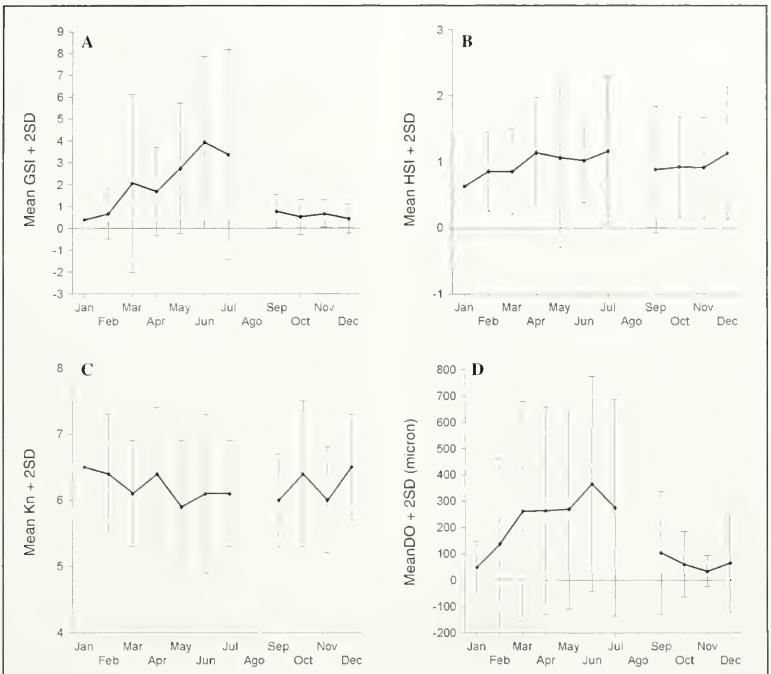

Figure 3

Monthly variation of the mean and standard deviation (SD) of the gonadosomatic index (GSI) (**A**), hepatosomatic index (HIS) (**B**), and condition factor (kn) (**C**) and oocyte diameter (DO) (**D**) in the blacktail comber (*Serranus atricauda*) from the Canary Islands.

Regression analysis showed significant positive correlation between annual fecundity and total length, total weight, and gutted weight. Total weight was the best predictor of annual fecundity ($PAFE$=1,053,504.23×1.0 0^{TW}; r^2=0.764, P<0.01, n=28); followed by total length ($PAFE$=63,648×4351×1380^{TL}; r^2=0.752, P<0.01, n=28); and gutted weight ($PAFE$=1,055,580×1.00^{GW}; r^2=0.723, P<0.01, n=28) (Fig. 6, A–C).

Discussion

The histological description of gonad structure is fundamental to understanding reproduction. In most reproductive fish studies the histological technique is omitted because it is too expensive and time-consuming. Consequently, in many cases knowledge of reproduction is limited or biased (or is both) (García-Díaz et al., 2001).

The spawning period in teleosts is determined from changes occurring within the gonad throughout the year. The macroscopic or histological observations of the

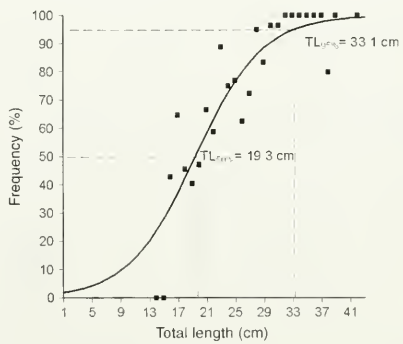

Figure 4

Sexual maturity curve and sizes at maturity for blacktail comber (*Serraus atricauda*) from the Canary Islands.

gonad (qualitative methods), somatic indices (e.g., GSI, HIS, and Kn), or evolution of oocyte diameter (quantitative methods) (or all four methods) are commonly applied. Many authors have disagreed about their applications and biological interpretation (De Vlaming et al., 1982; Wootton, 1990; Shapiro et al., 1993; Sadovy, 1996; Karlou-Riga and Economidis, 1997). Our results demonstrate that the GSI indicates only the spawning peak and not the presence of batch or multiple spawning within the species; and the HSI and Kn do not exhibit a clear trend throughout the year. Normally, variations of these indices (HSI and Kn) imply energy storage for reproduction (Hoar et al., 1983; N'Da and Déniel, 1993). However, *S. atricauda* does not require such storage because feeding activity is not altered during the reproductive period (Morato et al., 2000). Oocyte diameter presents a trend similar to that of GSI, although its biological interpretation is different. The oocyte may begin the vitellogenesis phase and there may be no significant increase in gonad weight. Consequently, GSI values do not necessarily change significantly when the spawning period has begun. Thus, the quantitative indices (GSI, HSI, Kn) show the general trend of the population, whereas the oocyte diameter provides information about the population as a whole, as well as at the individual level.

The analysis of qualitative and quantitative data in *S. atricauda* seems to indicate that spawning takes place throughout the year, although the general population spawns between March and July. In the Canary Islands, other members of the genus spawn over long periods: eight months in *S. cabrilla* and nine months in *S. scriba* (García-Díaz et al., 1997; García-Díaz 2003). These three species have the longest spawning season of all fish studied in the Canaries, although they are also the only species whose reproductive patterns have been analyzed with histological procedures. Nevertheless, environmental or biological factors (or both) must be related to this extended spawning period.

To estimate spawning frequency, the hydrated oocyte method is less time consuming but the POF method is better because the spatial and temporal distribution of the postovulatory follicle structures is not continuous (Hunter and Goldberg, 1980). Reproductive potential measured as potential annual fecundity has not been addressed in any species of the genus *Serranus* with the POF method to date. It is true that this fecundity must be considered as a rough estimation because the spawning frequency was a preliminary estimation because of the scarce number of individuals in sampling months. Siau and Bouian (1994) calculated the total fecundity in *S. cabrilla* and *S. scriba,* considering all the vitellogenesis oocytes. Their method has been widely rejected because it is valid only for

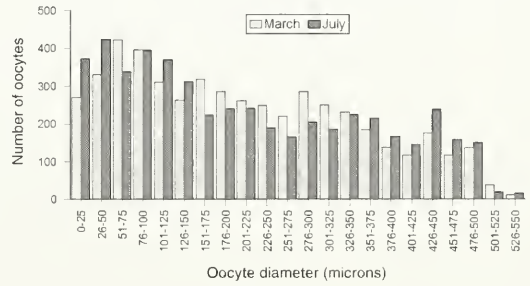

Figure 5

Oocyte size-frequency distributions (25-μm intervals) for blacktail comber (*Serraus atricauda*) ovaries from the Canary Islands.

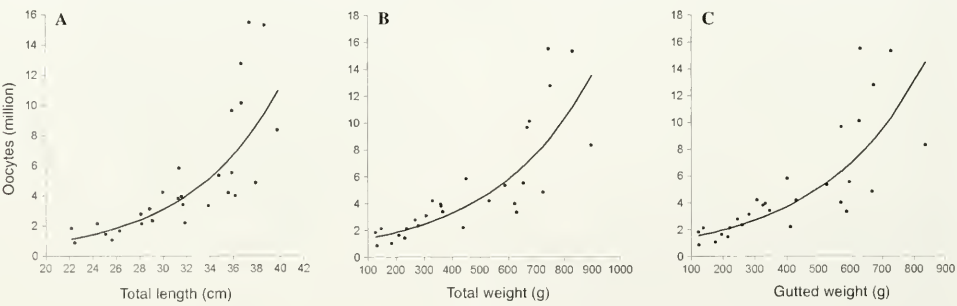

Figure 6

Relationships between potential annual fecundity and total length (**A**), total weight (**B**), and gutted weight (**C**) for blacktail comber (*Serranus atricauda*) from the Canary Islands.

determinate spawners, and both the above-mentioned serranids are indeterminate spawners (García-Díaz et al., 1997; García-Díaz, 2003). The fact that the method was used for these two indeterminate spawners could explain why the values of maximum fecundity obtained by these authors for *S. cabrilla* (441,502 oocytes) and *S. scriba* (54,649 oocytes) were lower than that for *S. atricauda* (15,5 millions oocytes). Consequently, the present study enables us to provide new reproductive data for blacktail comber, where potential annual fecundity is essential for future egg production models and estimates of spawning stock biomass.

Acknowledgments

We wish to thank José Ignacio Santana for the collection of samples, Antonio Valencia for his help in the building of the mechanism to separate the vitellogenic oocytes, Gordon Hamilton for proof reading the submission copy of the manuscript, and the reviewers for their comments and suggestions.

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Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral

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Abstract—There is increasing interest in the potential impacts that fishing activities have on megafaunal benthic invertebrates occurring in continental shelf and slope ecosystems. We examined how the structure, size, and high-density aggregations of invertebrates provided structural relief for fishes in continental shelf and slope ecosystems off southern California. We made 112 dives in a submersible at 32–320 m water depth, surveying a variety of habitats from high-relief rock to flat sand and mud. Using quantitative video transect methods, we made 12,360 observations of 15 structure-forming invertebrate taxa and 521,898 individuals. We estimated size and incidence of epizoic animals on 9105 sponges, black corals, and gorgonians. Size variation among structure-forming invertebrates was significant and 90% of the individuals were <0.5 m high. Less than 1% of the observations of organisms actually sheltering in or located on invertebrates involved fishes. From the analysis of spatial associations between fishes and large invertebrates, six of 108 fish species were found more often adjacent to invertebrate colonies than the number of fish predicted by the fish-density data from transects. This finding indicates that there may be spatial associations that do not necessarily include physical contact with the sponges and corals. However, the median distances between these six fish species and the invertebrates were not particularly small (1.0–5.5 m). Thus, it is likely that these fishes and invertebrates are present together in the same habitats but that there is not necessarily a functional relationship between these groups of organisms. Regardless of their associations with fishes, these invertebrates provide structure and diversity for continental shelf ecosystems off southern California and certainly deserve the attention of scientists undertaking future conservation efforts.

Manuscript submitted 8 December 2004 to the Scientific Editor's Office.

Manuscript approved for publication 21 July 2005 by the Scientific Editor.

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Science and conservation communities are increasingly interested in the potential impacts that fishing activities have on megafaunal benthic invertebrates found in continental shelf and slope ecosystems (Dayton et al., 2002; NRC, 2002; Malakoff, 2004; Roberts and Hirshfield, 2004; Rogers, 2004). Megafaunal invertebrates (>5 cm in height) contribute significantly to biodiversity, play important functional ecological roles, and can be indicators of long-term environmental conditions (e.g., Riedl, 1971; Palumbi, 1986; Brusca and Brusca, 1990). Moreover, because large invertebrates, such as sponges and corals, enhance the diversity and structural component of fish habitat and are vulnerable to impacts by at least some fisheries, they also may signify habitat areas of particular concern (HAPC) and as such would be protected under the Magnuson-Stevens Fishery Conservation and Management Act (Freese, 2001; Etnoyer and Morgan[1]).

[1] Etnoyer, P., and L. Morgan. 2003. Occurrences of habitat-forming deep sea corals in the Northeast Pacific Ocean. Technical Report, NOAA Office of Habitat Conservation, 31 p. Marine Biology Conservation Institute, 15806 NE 47th Ct., Redmond, WA 98052.

Deep-sea corals, such as gorgonians (sea fans), antipaththarians (black corals), scleractinians (stony corals), and hydrocorals, are of particular interest because they are often long-lived and slow-growing (Andrews et al., 2002; Heifetz, 2002), poorly studied (Etnoyer and Morgan[1]), and in certain situations vulnerable to human activities (e.g., mobile fishing gear) (Watling and Norse 1998; Freese et al., 1999; Krieger, 2001; Dayton et al., 2002; Fossa et al., 2002; NRC, 2002;). Other megafaunal invertebrates, such as crinoids, basket stars, and sponges also may enhance the structural components of fish habitat (Puniwai, 2002) and may be disturbed or destroyed by some fishing activities (Freese, 2001; Krieger, 2001).

The potential for invertebrates to add functional structure to benthic communities has centered largely around their size and complex morphology. A size threshold of 1 m has often been used as an indicator of structure-forming species because marked changes in benthic community structure have been observed in areas where rocky substrata exceed 1 m (Lissner and Benech, 1993). The complex structure of deep-sea corals also has been discussed as an important factor that contributes to microhabitat diversity (Krieger and Wing, 2002; Etnoyer and Morgan[1]). In this article, besides forming complex structure and large size, we also believe that megafaunal invertebrates form structure if they aggregate in high numbers, especially in areas of low relief. For example, aggregations of sea urchins and sea pens may provide significant structural relief for fishes in mud- and sand-dominated habitats (Brodeur, 2001).

An important question is the extent to which structure-forming invertebrates are ecologically important to fishes, especially those of economical value. Most studies have focused on "associations" between structure-forming invertebrates and fishes as a measure of ecological importance at several spatial scales. Fishes have been considered to be associated with invertebrates if they are found in the same trawl sample (Heifetz, 2002), if fishing is higher in areas with corals than without corals (Husebo et al., 2002), if they are found together within similar habitats observed from a submersible (Hixon et al.[2]), or if they are observed "among or within 1 m" from corals (Krieger and Wing, 2002). In this article we investigated association at three different levels: 1) fishes that are physically touching large invertebrates; 2) fishes that are found statistically more frequently near large invertebrates in relation to their overall abundance patterns; and 3) fishes that are found as nearest neighbors to large invertebrates.

The goal of this study was to describe patterns in the density, distribution, and size of structure-forming megafaunal invertebrates on deep rocky banks and outcrops off southern California. Given the recent interest in these organisms as potentially important habitat for groundfishes, and thus targets for protection from fishing activities, these organisms deserve a critical examination of their potential to contribute structure to continental shelf and slope ecosystems and an examination of their associations with fishes and other marine organisms. Accordingly, our specific objectives were the following:

- Identify structure-forming invertebrates based on criteria of size, morphological complexity, and density;
- Quantify the density and size distributions of these invertebrates according to depth and substratum types;
- Quantify associations between large, structure-forming invertebrates and other organisms, particularly fishes; and
- Assess the health of these organisms in terms of obvious physical damage.

Materials and methods

Underwater surveys were conducted off southern California by using nonextractive video-transect methods and direct observations from an occupied research submersible (*Delta*) from 8 October to 6 November 2002. These surveys were conducted as part of a larger investigation into the abundance, size, and distribution of cowcod (*Sebastes levis*) and associated benthic fishes and habitats inside and around the newly established Cowcod Conservation Areas (CCAs) off southern California (Fig. 1). The CCAs, which encompass 14,750 km^2 and are closed to groundfish harvest in water depth >37 m, were established in 2001 to assist in rebuilding the depleted cowcod population off southern California.

Digital, georeferenced maps of seafloor substratum types, interpreted from side-scan sonar, multibeam bathymetry, seismic reflection, and other past geophysical surveys, were used to identify and select sites of rocky habitats (Greene et al.[3]). We attempted to restrict the substratum types to mixed sediment and rock and to 30–330 m depth (i.e., likely cowcod habitat).

The *Delta* submersible was tracked by using an ORE Trackpoint II plus (ORE Offshore, West Wareham, MA) USBL system and WINFROG (vers. 3.1, FUGRO, San Diego, CA) software. We linked the tracking system to our ArcView® GIS (vers. 3.2, ESRI Corp., Redlands, CA) seafloor mapping project and tracked the submersible real-time in relationship to depth and seafloor habitat maps.

[2] Hixon, M. A., B. N. Tissot, and W. G. Pearcy. 1991. Fish assemblages of rocky banks of the Pacific northwest, Heceta, Coquille, and Daisy Banks. OCS Study MMS 91-0052, 410 p. U.S.D.I. Minerals Management Service 770 Paseo Camarillo, 2nd Floor, Camarillo, CA 93010.

[3] Greene, H. G., J. J. Bizzarro, D. M. Erdey, H. Lopez, L. Murai, S Watt, and J. Tilden. 2003. Essential fish habitat characterization and mapping of California continental margin. Moss Landing Marine Laboratories Technical Publication Series No. 2003-01, 29 p., 2 CDs. Moss Landing Marine Laboratories, 8272 Moss Landing Rd., Moss Landing, CA 95039.

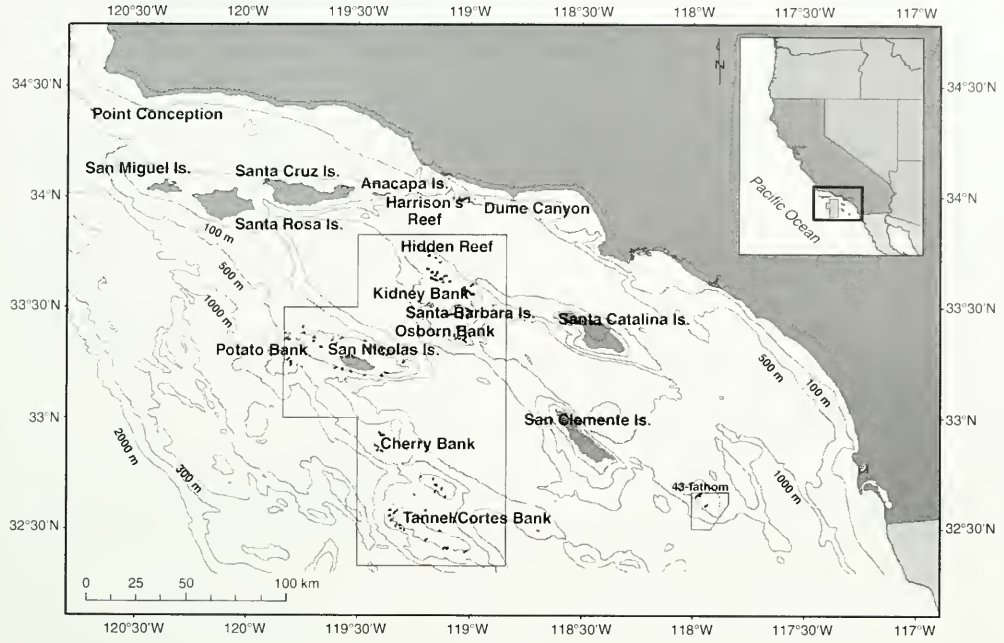

Figure 1

Locations of survey sites and dives (black dots) conducted inside and outside the cowcod conservation areas (delineated by outlined boxes) off southern California in 2002 to ascertain patterns in the density, distribution, and size of habitat-forming invertebrates.

We documented dives continuously during daytime hours with an externally mounted high-8 video camera positioned above the middle viewing-porthole on the starboard side of the submersible. The observer verbally annotated all tapes with observations on fishes, invertebrates, and physical habitats. Two parallel lasers were installed 20 cm apart on either side of the external video camera for estimating fish and invertebrate sizes and delineating a 2 m-wide belt transect for counting fishes and invertebrates. We used personal dive sonar from inside the submersible to verify the width of swath for the belt transects. Digital still and video cameras were used inside the submersible to help document fishes, invertebrates, and habitats.

We defined "habitat" using a combination of nine different categories of substratum and standard geological definitions (see Stein et al., 1992; Yoklavich et al., 2000). In order of increasing particle size or relief, these substrata were the following: mud (code M), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), continuous flat rock (F), rock ridge (R), and pinnacles (T). A two-character code was assigned each time a distinct change in substratum type was noted along the transect, thus delineating habitat patches of uniform type. The first character in the code represented the substratum that accounted for at least 50% of the patch, and the second character represented the substratum accounting for at least 20% of the patch (e.g., "BC" represented a patch with at least 50% cover by boulders and at least 20% cover by cobble). Each habitat patch also was assigned a code based on the degree of its three-dimensional structure as defined by the vertical relief of the physical substrata from the seafloor. Habitats were coded as 1=low (<1 m), 2=moderate (1–5 m), or 3=high relief (>5 m). Patches less than 10 seconds in duration were not recorded. The area of each habitat patch was determined by calculating the distance between the beginning and end of habitat patches with ArcGIS® and multiplying by the width of the transect (2 m).

A total of 58 different types of habitat patches were observed across all dives. These data were analyzed by a cluster analysis (Euclidean distance, group average method) by using the abundances of the 20 most common invertebrate species, and the resulting dendrogram was used to pool the number of codes into the 17 most distinct habitat types exhibiting a similarity of >50%.

Direct counts of megafaunal invertebrates were made from videotapes within each habitat patch; patch areas varied from 12–1472 m^2. Densities of invertebrates were estimated by dividing the total number of individuals

Table 1

Number of submersible dives and habitat patches surveyed for structure-forming invertebrates on rocky outcrops inside and outside the cowcod conservation areas in the southern California borderland.

Study site	No. of dives	No. of habitat patches
Inside the cowcod conservation areas		
43-fathom	4	142
Cherry Bank	8	266
Hidden Reef	5	156
Kidney Bank	21	474
Osborn Bank	5	199
Potato Bank	4	113
San Nicolas Island	23	785
Santa Barbara Island	9	203
Tanner and Cortes banks	21	587
Outside cowcod conservation areas		
Harrison's Reef	9	198
Dume Canyon	3	66
Total	112	3189

in each group, identified to the lowest taxonomic level, by the area of their associated habitat patches. For the larger invertebrates we recorded the geographic position and estimated maximum height of each solitary sponge, gorgonian, and black coral. We also noted the color of black corals. We made observations on the occurrence of animals (i.e., epizoids) found directly on sponges, gorgonians, and black corals, and also noted any damaged or dead individuals. Voucher specimens were collected to assist in taxonomic identification.

To quantify fish-invertebrate associations we used ArcGIS® to estimate the distance between each sponge, gorgonian, and black coral invertebrate and the nearest fish. These data were compared to the total number of fishes counted in habitats that contained sponges, gorgonians, and black corals by using a chi-square test to look for significant differences in the frequency of fish observed near corals in relation to overall fish abundance.

Results

We completed 112 dives and surveyed 3189 habitat patches (Table 1), covering 26.1 hectares at 32–320 m depths (median depth of 110 m). The distributions of number of patches and of surface area of habitats were similar except for sand (SS), sand-gravel (SG), and mud (MM) habitats, all of which had greater surface areas in relation to number of patches (Fig. 2, A and B). Overall, cobble-sand (CS), sand, mud, and sand-gravel

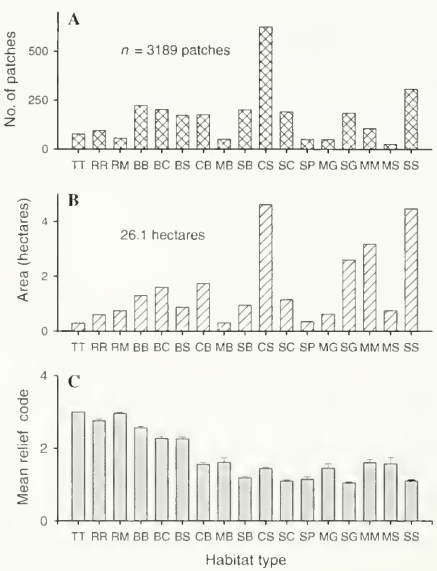

Figure 2

Characteristics of habitat patches surveyed on southern California rocky banks. (**A**) Number of patches in each substratum type. (**B**) Total area of each substratum type. (**C**) Mean relief (±1 standard error). See text for description of method and habitat codes. See page 169 for definitions for the substrate abbreviations along the *x* axis.

constituted the largest habitat areas, but cobble-sand and sand were the most frequent habitat types. Vertical physical structure varied among habitat types; the highest structure was found in high-relief rock areas (TT to BS) and lower structure was found in low-relief mixed rock (CB to SP) and mixed sediment areas (MG to SS; Fig. 2C). The frequency of patches of each substratum type varied by depth (Fig. 3). The incidence of most high-relief rock categories (TT, RR, BB, and BS) decreased with depth, and the occurrence of mud-dominated habitat patches (MB, MG, MS, MM) increased with depth.

Overall, 12,360 observations were made on 521,898 individuals from 15 taxa of megafaunal, structure-forming invertebrates; during these observations, estimates of size and incidence of epizoic animals on 9105 sponges, black corals, and gorgonians were made (Table 2). The most common structure-forming invertebrates (98% of total) included the crinoid *Florometra serratissima* (40%), the brittle star (*Ophiacantha* spp. [33%]), brachiopods (order Terebratulida [11%]), the white sea urchin (*Lytechinus anamesus* [9%]), the fragile sea urchin

(*Allocentrotus fragilis* [4%]), and sea pens (suborder Subselliflorae; [2%]; Fig. 4).

The density of common structure-forming invertebrates was variable across habitat types; some species were found over a wide range of habitats. Crinoids and basket stars were found on all 17 habitat types but were most dense on either high-relief rock or low-relief mixed rock (Fig. 5). In contrast, brittle stars and brachiopods were dense in low-relief mixed rock but rare or absent in low-relief mixed sediment. White sea urchins were most dense in habitats with sand, whereas fragile sea urchins were most dense in habitats with mud. White-plumed anemones were most dense in mud-gravel habitats, and sea pens were most dense in low-relief mixed-sediments (Fig. 5).

Deep sea corals and sponges were the largest structure-forming invertebrates but were relatively uncommon (2% of total) (Table 2). Gorgonians were difficult to distinguish and were categorized into one group (order Gorgonacea). The black coral is a new species that recently has been described and named the Christmas tree coral (*Antipathes dendrochristos*) (Opresko, 2005). Sponges were categorized into five groups based on their structure and shape: flat, barrel, shelf, vase, and foliose sponges (Fig. 6).

Gorgonians and black corals were most dense on low-relief mixed rock areas (Fig. 7). However, gorgonians were found in only four habitat types at 144–163 m depth, whereas black corals were found on 12 habitat types at 100–225 m depth, including pinnacle, boulder, and sand areas. These differences may be due to the unequal number of observations (i.e., 27 gorgonian vs. 135 black coral colonies).

The five morphological groups of sponges displayed broad distributions across habitat types but were especially dense on high-relief rock and low-relief mixed rock (Fig. 7). Flat, barrel, vase, and foliose sponges were found in all habitats; shelf sponges were found in all habitats except MM, MS, and SS. Foliose sponges were found at significantly deeper depths (mean=191 m; SE=53; n=1259) than were other sponge groups (pooled mean=152 m; SE=0.6; n=7545), which were not significantly different from each other (Kruskal-Wallis H=594; df=4; P<0.01). Generally sponge size increased with increasing depth, although the correlation was low (r=0.07; P<0.001; n=6551). Although sponges were found throughout the study area, gorgonians and black corals were restricted in their distribution to a small number of sites (Fig. 8).

Structure-forming invertebrates displayed wide variation in size; maximum height ranged from 4 cm for brachiopods to 2.5 m for black corals (Table 2). There was no significant correlation between size of the invertebrate taxa and structural relief of the substratum types (r=0.28, P=0.30, n=15).

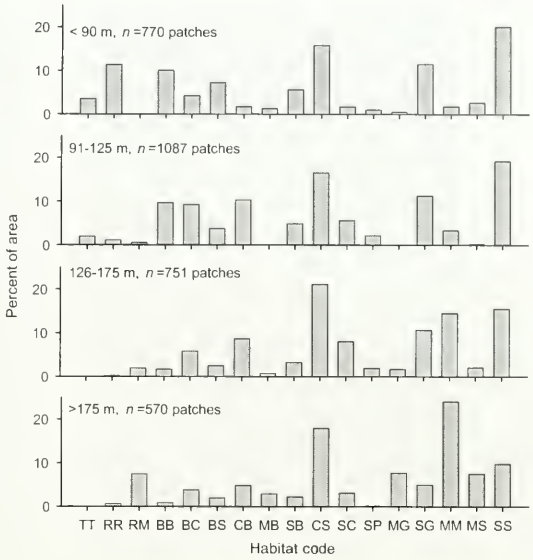

Figure 3

The frequency of habitat patches of each substratum type, stratified by depth. See page 169 for definitions for the substrate abbreviations along the x axis.

Gorgonians and black corals had different size distributions (Fig. 9). Black corals ranged from 10–250 cm in height (mean=33.6; SE=1.9; n=195) and most individuals were in the 10–50 cm size category. Individuals were found in three color forms: gray-to-white (50%), rusty-brown-to-red (47%), and gold (3%). Gorgonians ranged in size from 10 to 40 cm (mean=21.7; SE=1.2; n=27) and were found in multiple morphological forms from elongate to fan-like (Fig. 6).

Sponges displayed similar size distributions to those of gorgonian corals, but had different mean and maximum sizes (Fig. 9). Mean sizes of flat, barrel, and foliose sponges were not significantly different from each other (pooled mean=19.8 cm; SE=0.1; n=7373) but were significantly smaller than vase and shelf sponges (pooled mean=20.9 cm; SE=0.2; n=1289), which were not different from each other (one-way ANOVA; F=4.52; df=4,8657; P=0.001). The maximum observed height was 50 cm for shelf sponges, 60 cm for foliose sponges, and 100 cm for barrel, flat, and vase sponges (Fig. 9).

Most (98.2% by number) sponges, gorgonians, and black corals by number did not have any other organisms living on them (Table 3). Overall, crinoids (1.4%) were most commonly associated with these large invertebrates, followed by sponges (0.1%), and nine other

Table 2

Significant criteria of structure-forming invertebrates on rocky outcrops off southern California. "X" indicates taxa that exhibit large size, complex morphological shape, and high-density aggregations. SE is standard error and *n* is the total number of observations per taxon. The sample sizes for density and depth calculations were reduced because of incomplete observations on all individuals. Organisms are ordered from largest to smallest group.

		Criteria			Density (no./hectare)			Depth (m)		
Taxa	*n*	Size	Complex morphology	High density	Mean	SE	Maximum height (cm)	Mean	SE	Mean physical structural relief
Black coral (*Antipathes dendrochristos*)	135	X	X		10	4	250	183	24	1.7
Flat sponge	4240	X			312	53	100	149	43	1.9
Barrel sponge	2138	X			163	28	100	151	46	2.0
Vase sponge	1167	X			90	16	100	163	44	1.9
Sea pen (Subselliflorae)	9726	X		X	819	153	100	157	61	1.4
Basket star (*Gorgonocephalus eucnemis*)	733	X	X		58	12	90	162	44	1.7
White-plumed anemone (*Metridium farcimen*)	57	X			5	2	80	161	46	1.9
Foliose sponge	1259	X			96	25	60	191	53	2.0
Shelf sponge	139	X			10	3	50	158	47	2.1
Gorgonian (Gorgonacea)	27		X		3	3	40	159	4	1.2
Crinoid (*Florometra serratissima*)	174,231		X	X	22,045	8466	35	146	46	1.6
Brittle star (Ophiuridae)	207,667			X	17,786	4301	15	148	47	1.8
Fragile sea urchin (*Allocentrotus fragilis*)	18,363			X	2031	668	8	185	45	1.8
White sea urchin (*Lytechinus anamesus*)	45,092			X	4631	1388	4	85	20	1.2
Brachiopod (Order Terebratulida)	56,924			X	3623	1705	4	100	17	1.8

Table 3

Associations of organisms with large structure-forming invertebrates on rocky banks off southern California.

		Associated organisms (% of total observations)											
Taxa	*n*	None	Crinoids	Sponges	Fishes	Egg cases	Crabs	Basket stars	Brittle stars	Sea stars	Anemone	Algae	Salps
Foliose sponge	1262	99.0	0.6	0.3	0	0	0	0	0	0	0	0	0
Flat sponge	4043	99.5	0.5	<0.1	0	0	0	<0.1	0	0	0	0	0
Barrel sponge	2068	98.0	1.9	0	0	0	0	0	0.1	0.1	0	0	0
Shelf sponge	134	99.3	0.7	0	0	0	0	0	0	0	0	0	0
Vase sponge	1155	96.1	3.6	0	0.1	0.1	0	0.1	0	0	0	0	0
Gorgonian	27	100	0	0	0	0	0	0	0	0	0	0	0
Black coral	194	84.7	6.8	3.1	1.3	0	1.8	0.4	0.4	0	0.4	0.4	0.4
Total	8883	98.2	1.4	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

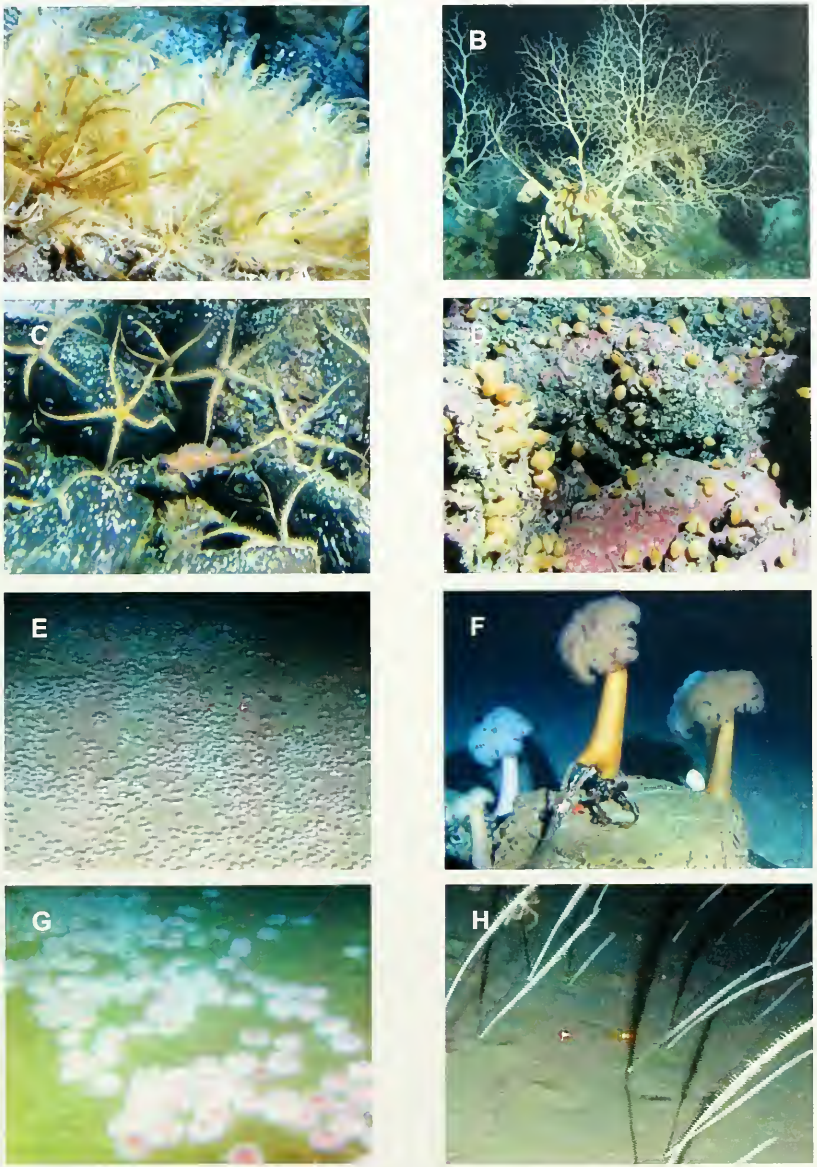

Figure 4

Some major structure-forming invertebrates on southern California rocky banks: (**A**) crinoids (*Florometra serratissima*), (**B**) basket stars (*Gorgonocephalus eucnemis*), (**C**) brittle stars (*Ophiacantha* spp.), (**D**) brachiopods (Terebratulida), (**E**) white sea urchins (*Lytechinus anamesus*), (**F**) white-plumed anemones (*Metridium farcimen*), (**G**) fragile sea urchins (*Allocentrotus fragilis*), and (**H**) sea pens (Subselliflorae).

taxa (all <0.1%). Black corals had the largest incidence of associated animals (15.3% of individuals), followed by vase (3.9%), barrel (2%), foliose (1%), shelf (0.7%), and flat (0.5%) sponges. Fish were most commonly observed on black corals (1.3%) but were also observed on vase sponges, including an attached egg case. No organisms were observed living on gorgonians.

The frequency of fish species near sponges, gorgonians, and black corals was significantly different from the frequency of those same species found elsewhere along transects (chi-square, all $P<0.01$; Table 4). Of the 108 species adjacent to these large invertebrates, six species were found at significantly higher frequencies than predicted by their density along transects: cowcod, bank rockfish (*Sebastes rufus*), swordspine rockfish (*Sebastes ensifer*), shortbelly rockfish (*Sebastes jordani*), pinkrose rockfish (*Sebastes simulator*), and members of the rockfish subgenus *Sebastomus* (Table 4).

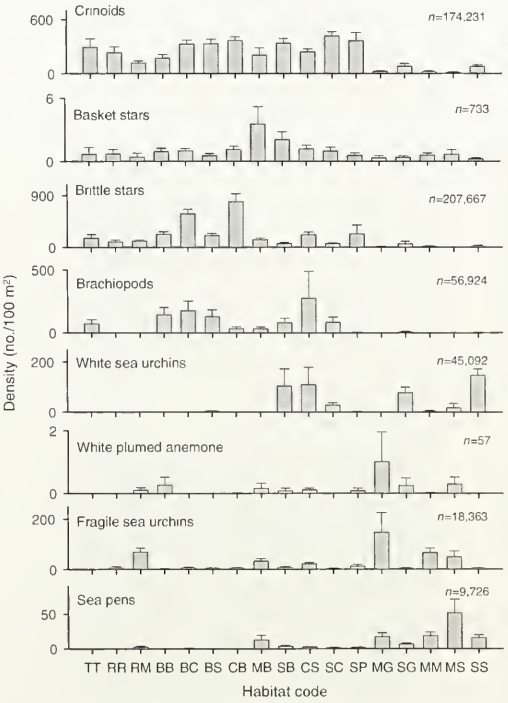

Figure 5

Mean density of structure-forming invertebrates in habitat patches of each substratum type. Vertical bars are ± one standard error. See page 169 for definitions for the substrate abbreviations along the *x* axis.

The distribution of mean nearest-neighbor distances between fishes and large invertebrates varied from 0.1 to 9.9 m (Fig. 10). Overall median distances varied from 0.9 m (shelf sponges) to 1.8 m (black corals). However, there were no statistical differences between the median distances for each group (Kruskal-Wallis, $H=10.4$; df=6; $P=0.11$). For the six fishes that were found more frequently near large invertebrates than on transects, the overall median distances to the invertebrates were 5.5 m (cowcod), 1.0 m (bank rockfish), 1.3 m (swordspine rockfish), 1.5 m (shortbelly rockfish), 1.7 m (pinkrose rockfish), and 1.4 m (*Sebastomus*).

The overall incidence of damaged and dead sponges, gorgonians, and black corals was low (0.3% of total number observed). Black corals were more commonly damaged (1.7%) or dead (1.1%), followed by vase sponges (0.6% and 0.1%, respectively), barrel sponges (0.5% and 0%), and foliose sponges (0% and 0.1%). No dead or damaged flat or shelf sponges or gorgonians were observed. Damage in black corals included portions of the colony that appeared discolored; dead black corals lacked polyps and were discolored. Among sponges, the most common damage was individuals that had broken from the substratum and were lying on their side or broken colonies.

Discussion

Several groups of invertebrates were distinguished by their large size, such as black corals, sponges, crinoids, basket stars, anemones, and sea pens. Organism size is an important aspect of structural habitat because it contributes to vertical relief and increases the availability of microhabitats. For example, yelloweye (*Sebastes ruberrimus*) rockfish may use the large gorgonian coral *Primnoa* as a vantage point to prey upon small fishes (Krieger and Wing, 2002). Size variation among structure-forming invertebrates was significant. Individual black corals, sea pens, and sponges greater than 1 m in height represented only 0.1% of all organisms, and 90% of the individuals were <0.5 m high.

Similarly, the complex structures of crinoids, gorgonians, black corals, and basket stars may increase the availability of microhabitats and create a high surface area for settlement or retention of other organisms. Fish egg cases have been observed attached to both gorgonians (Etnoyer and Morgan[1]) and vase sponges (present study, Table 3).

High-density aggregations have not been used as a criterion for defining structure-forming invertebrates, but there are several examples that illustrate the potential importance of these aggregations. High density "forests" of crinoids provide refuge and substrata for a wide variety of small fishes and invertebrates in rocky areas (Lissner and Benech, 1993; Puniwai, 2002).

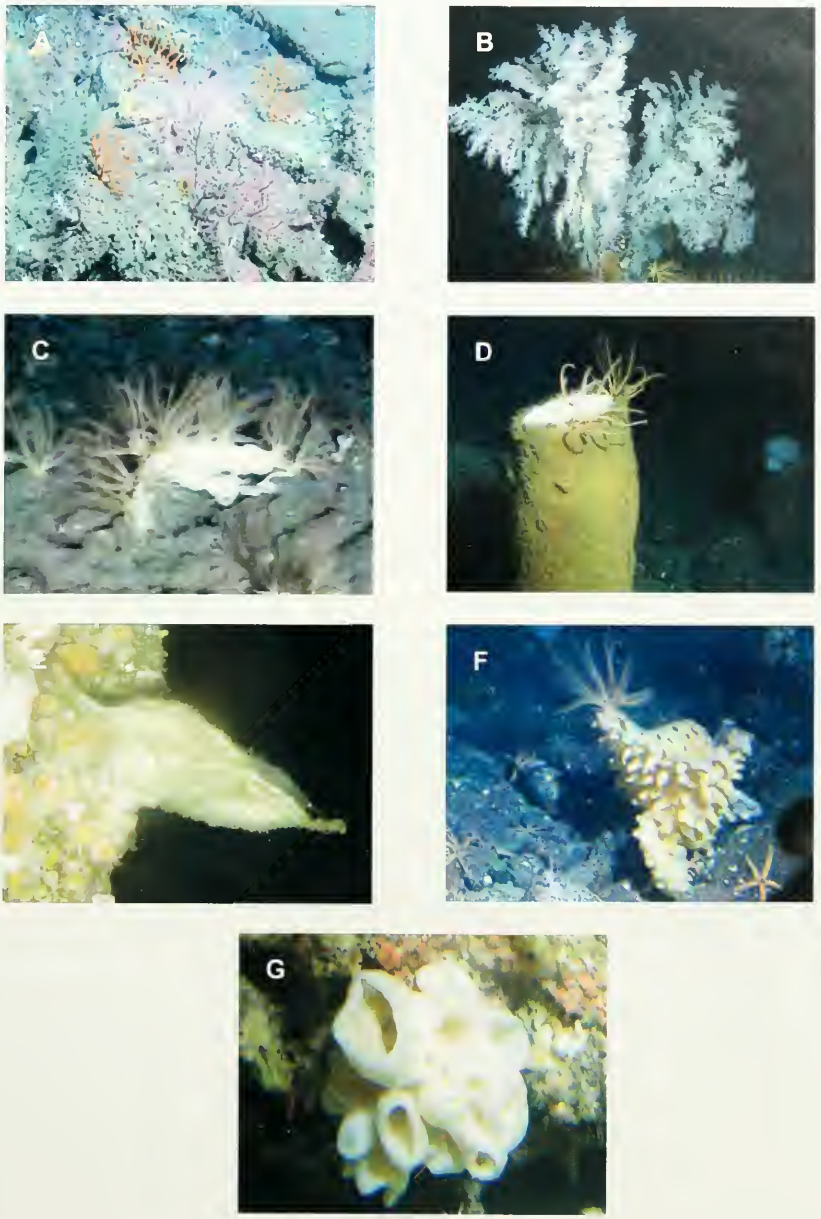

Figure 6

Structure-forming invertebrates: (**A**) gorgonians (Gorgonacea), (**B**) black coral (*Antipathes dendrochristos*), (**C**) flat, (**D**) barrel, (**E**) shelf, (**F**) vase, and (**G**) foliose sponges on southern California rocky banks.

Similarly, high-density aggregations of brittle stars and brachiopods in boulder-cobble areas and fields of sea pens and sea urchins in sand and mud habitats also may provide space and structure for other organisms (e.g., Brodeur, 2001).

With the exception of black corals and sea pens, the largest structure-forming invertebrates, such as sponges, *Metridium* spp., and crinoids, were most common on high- to moderate-relief rocky habitats. These long-lived organisms are likely to be favored in stable habitats that are more insulated from sediment transport and high particle loads than low-relief, mud-dominated areas (Lissner and Benech, 1993). Large invertebrates add structure and micro-scale complexity to these rocky habitats that already contain high-to-moderate amounts of relief. Sponges, with their broad distributions, may also provide structure for flatfishes in low-relief mud habitats (Ryer et al., 2004)

Black corals and gorgonians, in contrast, are more commonly found in current-swept areas near drop-offs and under ledges (Grigg, 1974; Parrish, 2004). In our study, these invertebrates were found in low-relief mixed cobble-boulder-sand habitats at 100–225 m depths, providing significant vertical structure for potential use by a wide variety of organisms.

Aggregations of sea pens and sea urchins may provide important structure in low-relief sand and mud habitats where there is little physical habitat complexity. In addition, these organisms may provide refuge for small planktonic and benthic invertebrates, which in turn may be preyed upon by fishes. They also may alter water current flow, thereby retaining nutrients and entraining plankton near the sediment. Urchins rapidly respond to patches of drift kelp (Harrold and Reed, 1985), which provide organic material to deep sea habitats (Harrold et al., 1998).

One of the central issues currently relevant to structure-forming invertebrates is the degree to which these species contribute to the spawning, breeding, feeding, or growth-to-maturity of economically important fishes. Although there are several studies that report fish-invertebrate associations within common habitats (Hixon et al.[2]), or make anecdotal or general observations on fish-invertebrate associations (e.g., Krieger and Wing, 2002), few studies have systemically quantified these relationships. In our study, for 9105 observations on the larger invertebrates found on southern California rocky banks only 1.8% of individuals had other organisms lying on or attached to them. Moreover, the vast majority of these organisms were other invertebrates, including crinoids, sponges, crabs, basket stars, brittle stars, seastars, anemones and salps. Less than 1% of the observations of organisms actually sheltering in or located on invertebrates involved fishes (a total of five individuals and one egg case), and most were observed on large black corals (Table 3). This result implies that fishes are not strongly associated with structure-forming invertebrates in the areas we surveyed off southern California.

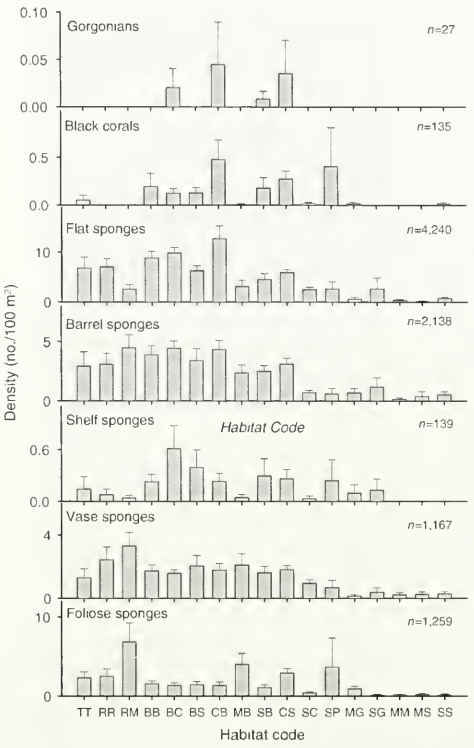

Figure 7

Mean density of gorgonians, black corals, and sponges in habitat patches of each substratum type. Vertical bars are ± one standard error. See page 169 for definitions for the substrate abbreviations along the *x* axis.

However, we should note that our observations were limited to daylight hours and that the viewing angle from the submersible generally precluded seeing inside some of the sponges (especially vase and barrel types). Moreover, our analyses focused on associations between fishes and individual solitary invertebrates, most of which were <0.5 m in height. We did not examine associations between all structure-forming invertebrates, nor did we examine associations between invertebrates and assemblages of fishes at the level of discrete habitat patches (100–1000 m scale) (e.g., Tissot et al.[4])

[4] Tissot, B. N., M. A. Hixon, D. L Stein. Unpubl. manuscript. Habitat-base submersible assessment of groundfish assemblages at Heceta Bank, Oregon from 1988–1990.

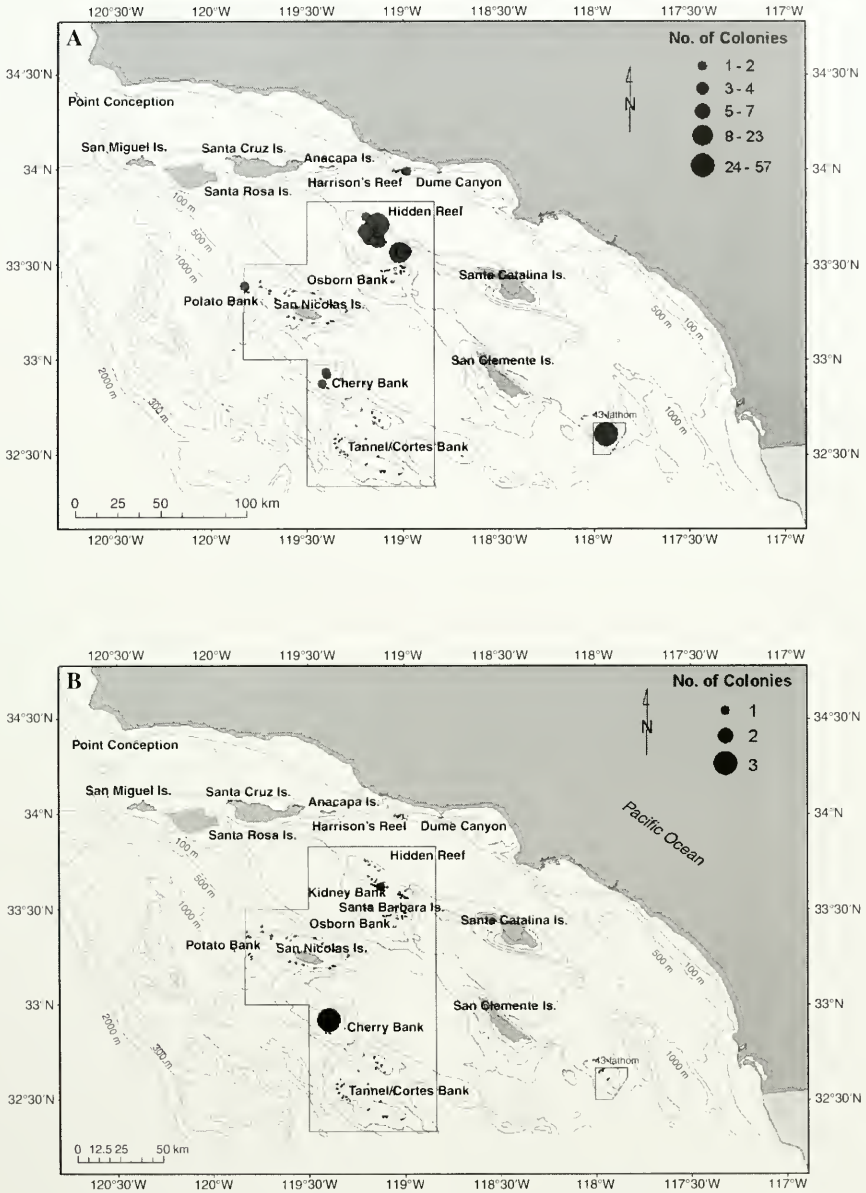

Figure 8

Distribution and number of (A) black coral and (B) gorgonian colonies inside and outside the cowcod conservation areas (delineated as outlined boxes) of southern California in 2002. Dive sites are indicated by black dots.

From the analysis of spatial associations between fishes and large, individual structure-forming invertebrates, six of 108 species were found more often adjacent to colonies than predicted by their abundance along transects. This result indicates that there may be spatial associations that do not necessarily include physical contact with the sponges and corals. However, the median distances between these six fish species and large invertebrates (1.0–5.5 m) were not particularly small. Thus, it is likely that these fishes and invertebrates are present in the same types of habitats and that there is not necessarily a functional relationship between these two groups of organisms.

Parrish (2004) reached similar conclusions on studies of black coral in Hawaii. Although fish densities were higher in areas that included corals, when bottom relief and depth were accounted for these densities were not higher than those for surrounding areas without corals. Thus, there was no clear evidence that corals served to aggregate fish. Rather, fishes and corals co-occurred in areas with similar physical relief and unique flow regime (Parrish, 2004). Auster (2005) also reached similar conclusions by finding no significant difference in the density of a common rockfish species (*Sebastes fasiatus*) between areas of rock and boulders with dense coral cover and similar areas having dense epifaunal cover (i.e., without coral). Auster concluded that although dense coral and dense epifaunal habitats were functionally equivalent, the epifaunal habitat was more widespread in his study area, making that habitat perhaps more important to the greater rockfish population. Finally, Syms and Jones (2001) demonstrated that removal of high densities of soft corals caused no significant changes in the associated fish communities and that the heterogeneity of habitat generated by soft corals was indistinguishable from equivalent habitat formed by rock alone. Thus, fish-invertebrate associations, by themselves, do not necessarily demonstrate the functional importance of invertebrates as habitat to benthic fish populations.

One possible conclusion from our study is that observed fish-invertebrate associations, like those reported for many cold-water corals, can be overstated. In the absence of quantitative information, observers may remember the few positive associations between fishes and structure-forming invertebrates but ignore (or forget) the more numerous observations of large invertebrates with no associated fishes. Indeed, the general impression of the authors after making submersible observations was that there were higher numbers of fishes associated with large invertebrates when in reality only five fishes were observed lying directly on a large invertebrate in the video transects. A more likely conclusion, however, is that the continental shelf communities of southern California are unique and that large black corals do not have the high number of commensals as seen, for example, on *Primnoa* in Alaska. An additional consideration is the relatively low number and size of individual sponges, gorgonians, and black corals observed in this study. *Primnoa* in Alaska can form massive stands 3 m tall and 7 m wide in some areas (Krieger and Wing, 2002). Moreover, the majority of fishes were observed on the largest individuals in their study (>15 m^3 in volume) Most of the corals in our study were <0.5 m in height. Given the importance of this issue, we argue for more rigorous quantitative studies on fish-invertebrate associations that would include densities of fishes and sizes of both fishes and invertebrates.

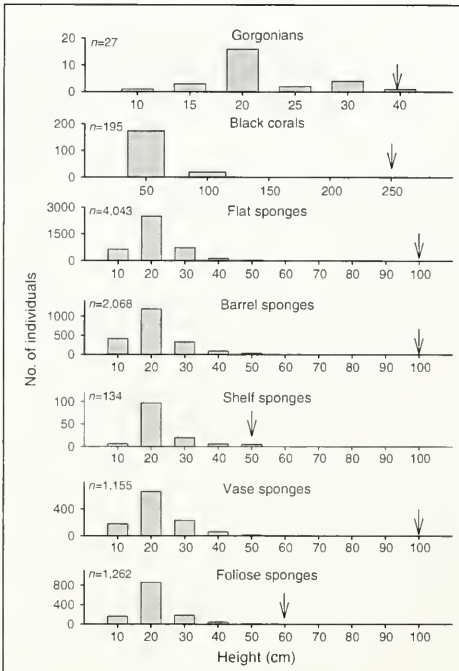

Figure 9

Size distributions of large, structure-forming invertebrates. Arrows indicate maximum sizes observed in each group.

Regardless of their associations with fishes, the structure-forming invertebrates described in this study are very likely to be ecologically important on continental shelf ecosystems and are certainly significant in their own right. Observation on the health of the larger invertebrates indicates few damaged (0.1%) or dead (0.2%) individuals and a low incidence of fishing gear in the areas surveyed (Tissot et al., unpubl, data). These observations are consistent with the absence of a significant commercial bottom trawling fishery in our survey area, which has been associated with negative impacts on large invertebrates in other locations (Watling and Norse, 1998; Freese et al. 1999; Krieger, 2001). Thus, this study affords a unique view of what appears to be

Table 4

Percentage of fish species near sponges, gorgonians, and black coral in relation to fishes counted along transects. Species that are less than 1% of the overall total number along all dives are not included. Species that were found more often near these invertebrates than expected by chance are indicated with an *.

	Common sponges					Shelf sponges		Gorgonians		Black coral	
Taxa	Total near tarrel sponges	Total near flat sponges	Total near foliose sponges	Total near vase sponges	Total on transect	Total near shelf sponges	Total on transect	Total near gorgonians	Total on transect	Total near black corals	Total on transect
Unknown *Sebastomus*	19*	17*	21*	16*	6	18*	6	0	7	38*	13
Swordspine rockfish *Sebastes ensifer*	16*	14*	15*	24*	6	16*	6	92*	31	23*	13
Pygmy rockfish *Sebastes wilsoni*	9	12	4	8	16	7	14	0	7	4	16
Pinkrose rockfish *Sebastes simulator*	6	5	13*	2	1	8	1	0	1	3	1
Squarespot rockfish *Sebastes hopkinsi*	6	9	2	4	24	4	24	0	30	4	17
Shortspine combfish *Zaniolepis frenata*	5	4	6	5	2	6	2	4	1	8	5
Bank rockfish *Sebastes rufus*	4*	3	6*	13*	1	5*	1	0	2	4	2
Halfbanded rockfish *Sebastes semicinctus*	2	5	2	0	3	5	3	0	<1	4	4
Unknown rockfishes *Sebastes* spp	4	4	3	1	2	3	2	0	2	4	2
Juvenile rockfish *Sebastes* spp	3	3	1	3	18	1	22	0	10	1	12
Shortbelly rockfish *Sebastes jordani*	2	2	4*	1	1	3	1	0	1	1	2
Unidentified combfishes *Zaniolepis* spp	2	2	2	2	1	3	1	0	1	1	2
Cowcod *Sebastes levis*	2	2	2	9*	<1	2*	<1	0	<1	2*	<1
Starry rockfish *Sebastes constellatus*	2	2	1	2	1	2	1	0	1	0	1
Greenstriped rockfish *Sebastes elongatus*	2	1	2	3	1	2	1	0	1	0	1
Rosy rockfish *Sebastes rosaceus*	2	2	2	1	1	2	1	0	0	0	<1

continued

Table 4 (continued)

Taxa	Common sponges					Shelf sponges		Gorgonians		Black coral	
	Total near tarrel sponges	Total near flat sponges	Total near foliose sponges	Total near vase sponges	Total on transect	Total near shelf sponges	Total on transect	Total near gorgonians	Total on transect	Total near black corals	Total on transect
Dwarf-red rockfish *Sebastes rufinanus*	1	2	<1	2	3	1	3	0	<1	0	<1
Greenspotted rockfish *Sebastes chlorostictus*	1	1	<1	1	1	1	<1	0	<1	1	<1
Blackeye goby *Rhinogobiops nicholsii*	1	2	<1	0	4	<1	3	4	1	0	<1
Lingcod *Ophiodon elongatus*	2	1	1	0	<1	1	<1	0	<1	0	<1
Bocaccio *Sebastes paucispinis*	1	1	1	2	1	1	1	0	1	0	<1

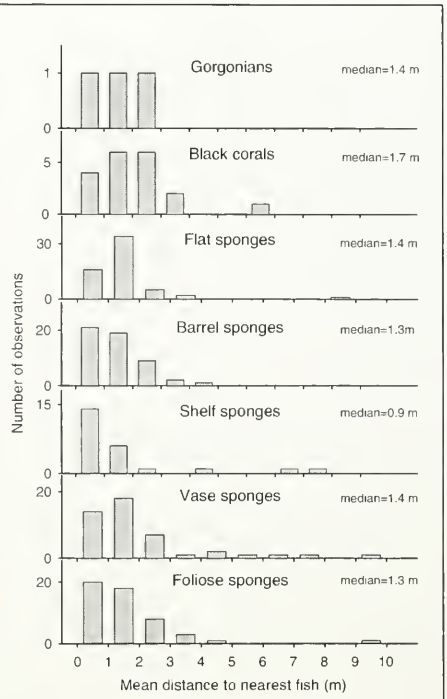

Figure 10

Mean nearest neighbor distances of fish species to gorgonians, black corals, and sponges.

relatively undisturbed megafaunal invertebrate communities in the southern California Borderlands, and supports the continued protection of these animals within the Cowcod Conservation Areas.

Acknowledgments

We thank the dedicated crews of the RV *Velero* and *Delta* for support in the field. D. Schroeder, M. Nishimoto, L. Snook, T. Laidig, T.Anderson, R. Starr, B. Lea, and C. Wahle assisted with the survey work. K. Greenwood and S. Green assisted with habitat and invertebrate analyses. Funding was provided by NOAA Fisheries, SWFSC Fisheries Ecology Division, Offices of Habitat Conservation and Protected Resources; the National Undersea Research Program; NOAA Marine Protected Area Science Center; the David and Lucile Packard Foundation; Washington State University Vancouver; and the Monterey Bay Sanctuary Foundation.

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Abstract—Larval and juvenile rockfishes (*Sebastes* spp.) are difficult to identify using morphological characters. We developed a key based on sizes of restriction endonuclease fragments of the NADH dehydrogenase-3 and -4 (ND3/ND4) and 12S and 16S ribosomal RNA (12S/16S) mitochondrial regions. The key makes use of variation in the ND3/ND4 region. Restriction endonuclease *Dde* I variation can corroborate identifications, as can 12S/16S variation. The key, based on 71 species, includes most North American taxa, several Asian species, and *Sebastolobus alascanus* and *Helicolenus hilgendorfi* that are closely related to rockfishes. Fifty-eight of 71 rockfish species in our database can be distinguished unequivocally, using one to five restriction enzymes; identities of the remaining species are narrowed to small groups: 1) *S. polyspinis*, *S. crameri*, and *S. ciliatus or variabilis* (the two species could not be distinguished and were considered as a single species); 2) *S. chlorostictus*, *S. eos*, and *S. rosenblatti*; 3) *S. entomelas* and *S. mystinus*; 4) *S. emphaeus*, *S. variegatus*, and *S. wilsoni*; and 5) *S. carnatus* and *S. chrysomelas*.

A key to selected rockfishes (*Sebastes* spp.) based on mitochondrial DNA restriction fragment analysis

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Manuscript submitted 11 October 2004 to the Scientific Editor's Office.

Manuscript accepted for publication 1 August 2005 by the Scientific Editor.

Fish. Bull. 104:182–196 (2006).

More than 100 species of rockfishes (genus *Sebastes*) are found worldwide (Kendall, 2000), and the majority are distributed along the Pacific coast of North America and in the northwest Pacific from the western Bering Sea south to Japan and Korea (Love et al., 2002). Sixty-five rockfish species are found along the California coast (Moser, 1996). Within the genus, there is a high degree of similarity of the morphological characters among many species. These similarities are in part due to recent divergence but also may have resulted from convergence of congeners occupying similar habitats.

Historically, species identification of *Sebastes* has been based on morphology; however, this approach is often insufficient, especially for identifying sympatric species, where there is considerable similarity in size and physical features and in pigmentation, as well as overlap in meristic characters. The difficulty in identifying *Sebastes* to species level exists for all developmental stages, but larvae are especially difficult to identify because they lack diagnostic characters (Kendall, 1991). Currently, only 15 species at the larval stage can be separated by physical characters such as body shape, pigmentation patterns, and head spine development (Love et al., 2002).

Rockfishes are important ecologically, and most species are economically valuable. *Sebastes* larvae form a large portion of ichthyoplankton collections and rank third or fourth in abundance among all fish larvae taken during California Cooperative Fisheries Investigations (CalCOFI) surveys that have covered the entire length of the California and Baja California coast and now cover waters off southern California. The ability to identify *Sebastes* accurately and efficiently at all developmental stages will greatly improve both our ability to learn about their life histories and our management and conservation ef-

forts. An increased understanding of life history variation can improve the systematic descriptions of *Sebastes* species, which has mostly been based on morphology.

Several methods have been developed to obtain species-specific information that supplements the use of morphological and meristic characters for species identification. Otolith microstructure and other hard structures have been used to distinguish the late-stage larvae and young-of-the-year pelagic juveniles of some *Sebastes* species (Laidig and Adams[1]; Laidig and Ralston, 1994; Laidig et al., 1996). Biochemical genetic methods have been used to identify adults (Barrett et al., 1966; Seeb, 1986), and may also be used to identify juveniles of some species (Seeb and Kendall, 1991). LeClair and Buckley (2001) used allozyme variation at 37 loci to positively identify 155 individuals of juvenile *Sebastes diploproa* and *Sebastes melanops*; but they were unable to identify another 29 individuals, partly because of a limited database. Despite some success with their use, allozymes often have low resolution, and there are complexes of species that cannot be distinguished by using allozymes alone (Seeb and Kendall, 1991).

DNA sequence-based methods have some advantages over the use of allozymes for the identification of juvenile fish species. They often have greater resolution, due in part to the fact that expression of some metabolic enzymes changes during development, whereas DNA sequences generally do not. DNA is less susceptible to degradation than the enzymes used in allozyme studies. Also, DNA sequence-based methods require a small amount of tissue sample, which is especially suited for work with samples from early life stages (e.g., Gray et al., 2006). Because it has a relatively high rate of substitution (Moritz et al., 1987), mitochondrial DNA (mtDNA) can be useful for distinguishing closely related species. Mitochondrial DNA is usually inherited maternally in vertebrates and does not recombine with paternal mtDNA if it is leaked into the zygote (Gyllensten et al., 1991; but see Rokas et al., 2003). Thus, the mtDNA sequence represents a matrilineal phylogeny and is often useful in delineating phylogenetic relationships of closely related species. Sequences of the mitochondrial cytochrome *b* gene were used to identify the pelagic young of *Sebastes constellatus* and *Sebastes ensifer* (Rocha-Olivares et al., 2000). Multiplex PCR of haplotype-specific regions of mtDNA has also been used to identify early stages of *Sebastes* species (Rocha-Olivares, 1998).

The objective of this study was to devise a key for species identification using mtDNA restriction fragment data from both the ND3/ND4 and 12S/16S regions. In a previous study, data for species-specific mtDNA restriction site variation in the ND3/ND4 region were presented for 15 *Sebastes* species (Gharrett et al., 2000). We have included data for 56 additional species using the ND3/ND4 and 12S/16S regions of the mtDNA as the target region of PCR-amplification. We have included specimens of *Helicolenus hilgendorfi* and *Sebastolobus alascanus* for contrast.

Materials and methods

Adult specimens of 71 species of rockfishes were collected from the Gulf of Alaska, the coastal waters of California and Baja California, and from the coast of Japan. Samples of *H. hilgendorfi* and *Sebastolobus alascanus*, species from two sister genera, were collected from Japanese coastal waters and the Gulf of Alaska, respectively, to provide outgroup comparisons. A sample of heart tissue from each specimen was preserved in either 95% ethanol or a solution that was 80% 0.25M ethylenediaminetetraacetic (EDTA) acid at pH 8 and saturated with NaCl (Seutin et al., 1991) and 20% dimethyl sulfoxide (DMSO). At least five individuals of each species were analyzed, except for a few species for which less than five specimens were available. We did not distinguish between *S. ciliatus* and *S. variabilis*, which had not yet been described (Orr and Blackburn, 2004), when we collected samples.

Total genomic DNA was isolated by using a Purgene DNA™ isolation kit (Gentra Systems, Inc., Minneapolis, MN). Two target regions of mtDNA were amplified by using the polymerase chain reaction. The ND3/ND4 region begins in the glycyl tRNA gene and spans the NADH-dehydrogenase subunit-3, arginyl tRNA, NADH-dehydrogenase subunit-4L, and NADH-dehydrogenase subunit-4 genes, ending in the histidyl tRNA gene. The 12S/16S region starts near the phenylalanyl tRNA end of the 12S rRNA gene, and runs through the valyl tRNA gene to near the leucyl tRNA end of the 16S rRNA gene. Primers for target regions have been used to amplify these regions in northern Pacific rockfish (Gharrett et al., 2001). The lengths for the amplified ND3/ND4 and 12S/16S regions are about 2385 and 2430 base pairs, respectively, based on the aggregate restriction maps.

Subsamples of the PCR products of each individual were digested with one or more of the restriction endonucleases *Bst*N I, *Bst*U I, *Cfo* I, *Dde* I, *Hin*d II, *Hin*f I, *Mbo* I, *Msp* I, *Rsa* I, and *Sty* I. Fragments were separated electrophoretically in 1.5% agarose gels (one part agarose [Sigma-Aldrich, St. Louis, MO] and two parts Synergel™ [Diversified Biotech Inc., Boston MA]) in 0.5×TBE buffer (TBE is 90mM Tris-boric acid, and 2 mm EDTA, pH 7.5). A 100 base-pair ladder provided molecular weight markers to estimate restriction fragment sizes. Gels were stained with ethidium bromide and photographed on an ultraviolet light transilluminator. Restriction fragments that could not be accurately measured from agarose gels were separated on 8% polyacrylamide gels and stained with SYBR Green I Nucleic Acid Stain™ (Molecular Probes, Eugene, OR) using a 25-bp ladder for a molecular weight standard.

[1] Laidig, T. E., and P. B. Adams (eds.). 1991. Methods used to identify pelagic juvenile rockfish (genus *Sebastes*) occurring along the coast of central California. NOAA-TM-NMFS-SWFSC-166, 180 p. NMFS Southwest Fisheries Science Center, 110 Shaffer Rd., Santa Cruz, CA 95060.

A restriction site map was created for each endonuclease by using all observed restriction fragment patterns and necessary double digests.

Results

Baseline data

Interspecific variation was observed for all enzymes in both mitochondrial regions, except for *Hin*d II in the 12S/16S region. Intraspecific variation was observed for several enzymes. A total of 215 restriction sites were detected in the ND3/ND4 and 12S/16S regions (Appendix 1). Of the 215 sites, 97 were unique to *Sebastes* species, 21 were unique to *Sebastolobus alascanus*, seven were unique to *H. hilgendorfi*, and one was shared by *Sebastolobus alascanus* and *H. hilgendorfi*. The ND3/ND4 region had 141 sites, and the 12S/16S region had 74 sites. In the ND3/ND4 region, 36 sites were common in all haplotypes, whereas 46 occurred in only a single haplotype.

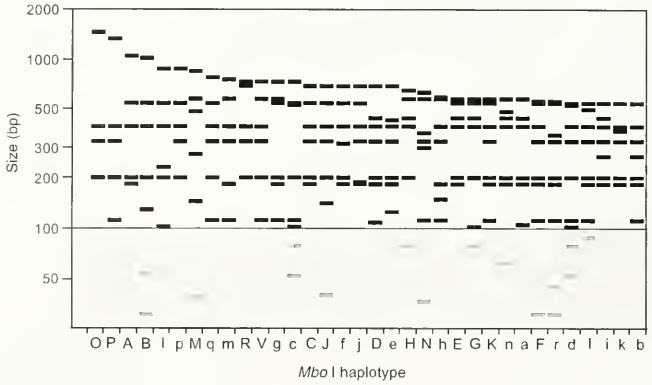

Figure 1

A mock gel showing expected fragment patterns for rockfish (*Sebastes* spp.) haplotypes as a result of digestion of the mitochondrial ND3/ND4 PCR product by restriction endonuclease *Mbo* I. The mobilities are the logarithm of the fragment sizes and separation was assumed to have taken place in 1.5% agarose gels (one part agarose and two parts Synergel™). The haplotypes correspond to the fragment sizes in Appendix 1 and to the haplotypes in Table 1 and the identification key. A haplotype may occur in more than one species. Most of the fragments that occurred in the shaded region would probably not be well resolved in an agarose gel.

A total of 132 composite haplotypes resulted from site differences in the two mtDNA regions (Table 1). The individuals of *Sebastes* species had 127 haplotypes; *Sebastolobus alascanus* had four haplotypes; and *H. hilgendorfi* had a single haplotype. Thirty-four of the 71 species displayed intraspecific variation and were represented by more than one composite haplotype; the remaining 37 species had a single composite haplotype.

Two pairs and three triplets of *Sebastes* species had identical composite haplotypes and could not be separated at the species level with this restriction site information (see identification key). These groups were 1) *S. carnatus* and *S. chrysomelas*; 2) *S. chlorostictus*, *S. eos*, and *S. rosenblatti*; 3) *S. ciliatus* or *variabilis*, *S. crameri*, and *S. polyspinis*; 4) *S. emphaeus*, *S. variegatus*, and *S. wilsoni*; and 5) *S. entomelas* and *S. mystinus*. Several pairs of haplotypes between variable *Sebastes* species were separated by a single restriction site. These included 1) *S. hopkinsi* and *S. ovalis*—*Dde* I; 2) *S. zacentrus* and the *S. emphaeus-S. variegatus-S. wilsoni* complex—*Rsa* I; and 3) *S. reedi* and the *S. ciliatus or variabilis-S. crameri-S. polyspinis* complex—*Mbo* I. The most variable species was *S. mystinus*, with five haplotypes. Five *Sebastes* species, *S. dalli*, *S. hubbsi*, *S. polyspinis*, *S. trivittatus*, and *S. zacentrus*, as well as *Sebastolobus alascanus*, had four haplotypes each. The remaining 58 *Sebastes* species have species-specific markers that allow unambiguous identification.

Use of the key

The key we developed for *Sebastes* species was based exclusively on variation in the ND3/ND4 region because it required only a single PCR amplification and variation in the 12S/16S region contributed no additional resolution between species to that provided by the ND3/ND4 region. The key is not a dichotomous key, but it is applied in the same way that taxonomic keys are applied. The first step is to digest PCR-amplified DNA from the ND3/ND4 region with restriction endonuclease *Mbo* I and to estimate the sizes of the fragments produced by separating the fragments on an agarose-Synergel™ gel. The best results will be achieved by using molecular weight markers, digitally photographing the gels, and estimating the fragment sizes with appropriate software. Alternatively, visual recognition of the fragment pattern can be accomplished by constructing a graphic key (e.g., Fig. 1 for *Mbo* I fragments) from fragment sizes predicted by the restriction site maps in Appendix 1. Note that in the figure, the logarithm of the size of the fragment (in base pairs) is used to estimate the mobility of a fragment (Sambrook et al., 1989). When the *Mbo* I haplotype has been identified, proceed to the next step. For example if the *Mbo* I digest results in haplotypes D or e, proceed to step g. in the key, which specifies digestion of another subsample of the ND3/ND4 PCR

Table 1

Composite haplotypes for *Sebastes* spp., *Helicolenus hilgendorfi*, and *Sebastolobus alascanus* in the ND3/ND4 and 12S/16S mtDNA regions. The haplotype codes refer to haplotypes in Appendix 1.

	ND3/ND4										12S/16S									
Species	*Bst*N I	*Bst*U I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sty* I	*Bst*N I	*Bst*U I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sty* I
aleutianus A	F	C	B	N	A	E	K	D	D	C	A	A	A	D	A	B	C	B	A	A
aleutianus B	F	C	B	N	A	F	K	D	D	C	A	A	A	D	A	B	C	B	A	A
alutus A	B	C	A	J	A	A	B	B	C	C	A	A	A	D	A	B	C	B	A	A
alutus B	B	C	A	J	A	A	B	B	C	C	A	A	A	D	A	A	C	B	A	A
atrovirens	O	B	D	b	C	G	j	C	B	I	A	A	A	D	A	B	A	A	A	A
auriculatus	F	B	D	v	A	G	k	C	B	A	A	A	A	D	A	B	A	A	A	A
aurora	B	C	D	m	A	A	b	L	A	e	A	A	A	D	A	A	C	B	A	A
babcocki A	F	C	D	G	A	A	G	B	B	C	A	A	A	C	A	B	C	B	B	A
babcocki B	F	C	D	F	A	A	H	B	B	C	A	A	A	C	A	B	C	B	B	A
barealis	F	C	D	D	A	A	F	B	B	C	B	A	A	A	A	B	C	A	C	A
brevispinis	G	C	D	C	A	A	K	D	B	D	A	A	A	D	A	A	C	A	C	A
capensis A	F	C	D	G	B	A	E	B	D	O	A	A	A	C	A	A	C	A	D	A
capensis B	F	C	D	F	B	A	E	B	D	O	A	A	A	C	A	A	A	A	D	A
capensis C	F	C	D	G	B	A	E	B	D	O	A	A	A	D	A	A	C	A	D	A
carnatus A	F	a	A	I	C	G	C	a	B	A	A	A	A	D	A	B	A	A	A	A
carnatus B	F	a	A	I	C	A	C	a	B	A	A	A	A	D	A	B	A	A	A	A
carnatus C	F	a	a	I	C	G	C	a	B	A	A	A	A	D	A	B	A	A	A	A
caurinus A	F	B	C	L	A	G	C	C	B	A	A	A	A	D	A	B	A	A	A	A
caurinus B	F	B	C	L	A	G	J	C	B	A	A	A	A	D	A	B	A	A	A	A
chlorosticus	F	B	D	G	B	A	E	B	C	C	A	A	A	C	A	B	C	A	D	A
chrysomelas A	F	a	A	I	C	G	C	a	B	A	A	A	A	D	A	B	A	A	A	A
chrysomelas B	F	a	A	I	C	G	C	a	B	A	A	A	A	D	A	B	A	A	C	A
ciliatus variabilis	A	D	A	M	A	A	F	B	F	C	A	A	A	D	A	B	C	A	A	A
constellatus A	F	C	D	G	F	A	E	E	D	M	G	A	A	C	A	A	C	E	D	A
constellatus B	F	C	D	G	F	A	E	E	D	M	A	A	A	C	A	A	C	A	D	A
crameri	A	D	A	M	A	A	F	B	F	C	A	A	A	D	A	B	C	A	A	A
dalli A	F	C	D	bb	b	G	p	C	B	g	A	A	A	D	A	H	A	A	A	A
dalli B	F	C	D	bb	b	G	l	C	B	g	A	A	A	D	A	H	A	A	A	A
dalli C	F	C	D	bb	b	G	p	C	a	b	A	A	A	D	A	H	A	A	A	A
dalli D	F	C	D	bb	b	G	p	C	B	g	A	A	A	D	A	B	A	A	A	A
diploproa	g	B	C	aa	A	A	C	M	C	C	A	A	A	C	A	B	G	F	A	A
elongatus A	W	C	I	h	A	A	C	M	P	C	A	A	A	D	A	B	I	A	A	A
elongatus B	W	C	I	h	A	A	A	M	P	C	A	A	A	D	A	B	I	A	A	A
emphaeus A	F	C	D	E	A	A	D	B	D	C	A	A	A	B	A	B	C	A	C	A
emphaeus B	F	C	D	E	A	A	D	B	B	C	A	A	A	B	A	B	C	A	C	A
ensifer A	F	C	D	F	B	Q	E	B	C	C	A	A	A	C	A	B	A	A	C	A
ensifer B	F	C	D	F	B	A	E	B	C	C	A	A	A	C	A	B	C	A	C	A
entomelas	F	C	J	I	A	A	E	a	B	C	A	A	A	D	A	A	A	F	B	A
eos	F	B	D	G	B	A	E	B	C	C	A	A	A	C	A	B	C	A	D	A
exsul	F	C	D	D	B	A	i	B	D	M	A	A	A	C	A	B	C	A	B	A
flavidus	E	C	D	H	A	C	A	B	A	C	A	A	A	A	A	B	C	B	D	A
gilli A	b	C	D	x	A	P	m	A	R	N	A	E	D	D	A	B	C	B	A	A
gilli B	b	C	D	x	A	P	K	A	R	N	A	E	D	D	A	B	C	B	A	A
goodei	Y	C	D	p	A	O	a	B	D	D	A	A	A	D	A	l	C	A	A	A
helvomaculatus A	F	C	D	K	B	A	A	B	C	C	A	A	A	C	A	B	B	A	D	A

continued

Table 1 (continued)

	ND3/ND4										12S/16S									
Species	*Bst*N I	*Bst*U I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sty* I	*Bst*N I	*Bst*U I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sty* I
helvomaculatus B	F	C	D	K	B	A	A	B	E	C	A	A	A	C	A	B	C	A	D	A
hopkinsi A	Z	C	A	n	A	g	K	B	C	e	A	A	A	C	A	B	C	A	B	A
hopkinsi B	Z	C	A	n	A	g	K	A	C	e	A	A	A	C	A	B	C	A	B	A
hopkinsi C	Z	C	A	u	A	g	g	B	C	e	A	A	A	C	A	A	C	A	B	A
hubbsi A	L	I	D	R	A	I	O	A	C	G	A	C	A	D	A	A	C	A	A	A
hubbsi B	M	I	D	S	A	I	O	A	C	G	A	C	A	D	A	A	C	A	A	A
hubbsi C	M	I	D	T	A	I	P	A	C	G	A	C	A	D	A	B	C	A	A	A
hubbsi D	M	I	D	S	A	F	O	A	C	G	A	C	A	D	A	A	C	A	A	A
inermis A	F	I	D	X	A	A	D	e	J	I	A	A	A	A	A	B	C	A	C	A
inermis B	F	H	D	X	A	A	D	e	J	I	A	A	A	A	A	B	C	A	C	A
inermis C	F	I	D	cc	A	I	D	e	J	I	A	A	A	A	A	B	C	A	C	A
jordani A	a	C	D	c	E	A	c	A	P	C	F	A	A	H	A	B	C	A	D	A
jordani B	a	C	D	c	E	A	d	A	P	C	F	A	A	H	A	B	C	A	D	A
jordani C	a	C	D	q	E	A	c	A	P	C	F	A	A	H	A	B	C	A	D	A
joyneri A	O	H	D	a	A	A	D	e	L	A	A	A	A	A	A	B	C	A	C	A
joyneri B	O	H	D	a	A	I	D	e	L	A	A	A	A	A	A	B	C	A	C	A
lentignosus	F	C	D	F	B	A	n	B	D	M	A	A	A	C	A	B	C	A	B	A
levis	B	A	g	d	A	A	q	d	B	C	A	A	A	D	A	B	C	A	D	A
macdonaldi	P	b	A	e	A	b	C	g	D	C	B	A	A	G	A	G	C	A	A	D
maliger	F	B	D	L	C	D	C	C	B	A	A	A	A	D	A	B	A	A	B	A
melanops A	D	C	D	F	A	B	E	A	A	C	A	A	A	D	A	B	C	B	D	A
melanops B	D	C	D	F	A	B	E	B	A	C	A	A	A	D	A	B	C	B	D	A
melanostomous A	O	C	D	g	A	A	K	A	O	C	A	A	A	D	A	B	C	B	C	A
melanostomous B	O	C	D	g	A	A	K	A	B	C	A	A	A	D	A	B	C	B	C	A
miniatus A	F	C	K	r	C	A	e	B	A	C	A	A	A	C	A	A	C	A	A	A
miniatus B	F	C	K	r	C	N	e	B	A	C	A	A	A	C	A	A	C	A	A	A
mystinus A	F	C	J	l	A	A	E	a	B	C	A	A	A	D	A	A	A	B	B	A
mystinus B	B	C	J	l	A	C	E	D	B	C	A	A	A	D	A	A	A	A	B	A
mystinus C	F	C	J	l	A	A	E	a	B	e	A	A	A	D	A	A	A	B	B	A
mystinus D	B	C	J	l	A	A	E	D	B	C	A	A	A	D	A	A	A	B	B	A
mystinus E	B	C	J	l	A	C	E	D	B	C	A	A	A	D	A	A	A	B	B	A
nebulosus A	F	G	A	Z	A	G	C	C	B	A	A	A	A	D	A	B	A	A	A	A
nebulosus B	F	G	A	Z	B	G	C	C	B	A	A	A	A	D	A	B	A	A	A	A
nigrocinctus	F	C	D	c	A	A	G	B	B	C	A	A	A	C	A	B	C	A	B	A
nivosus	N	A	D	U	A	I	C	B	I	A	A	A	A	G	A	A	C	A	A	C
ovalis	Z	C	A	*o*	A	g	K	B	C	e	A	A	A	C	A	B	C	A	B	A
paucispinis A	F	A	b	c	A	A	V	A	b	d	A	A	A	D	A	B	C	A	B	A
paucispinis B	F	A	b	c	g	A	V	A	b	d	A	A	A	D	A	B	C	A	B	A
phillipsi	B	C	D	m	A	A	b	B	B	e	A	A	A	D	A	B	C	B	A	A
pinniger	F	C	D	s	A	A	C	B	B	A	A	A	A	D	A	A	C	A	A	A
polyspinis A	A	D	A	M	A	A	F	B	F	C	A	A	A	D	A	B	C	A	A	A
polyspinis B	A	J	A	f	A	A	F	A	F	C	A	A	A	D	A	B	C	A	A	A
polyspinis C	A	D	A	M	A	A	F	B	F	C	A	A	A	I	A	B	C	A	A	A
polyspinis D	V	D	A	M	A	A	F	B	N	C	A	A	A	D	A	B	C	A	A	A
proriger	F	C	D	E	A	A	K	E	B	C	A	A	A	D	A	B	C	A	C	A
rastrelliger	c	C	C	v	A	a	A	C	B	A	A	A	A	D	A	B	A	A	A	A
reedi	A	D	A	M	A	A	r	B	F	C	A	A	A	D	A	B	C	A	A	A

continued

Table 1 (continued)

Species	ND3/ND4										12S/16S									
	BstN I	*BstU* I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sty* I	*BstN* I	*BstU* I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sty* I
rosaceus	F	C	D	k	B	A	E	B	B	C	A	A	A	C	A	B	C	A	B	A
rosenblatti	F	B	D	G	B	A	E	B	C	C	A	A	A	C	A	B	C	A	D	A
ruberrimus A	C	C	A	B	A	D	I	B	D	C	A	A	A	D	A	C	C	A	A	A
ruberrimus B	C	C	D	B	A	D	I	B	D	C	A	A	A	D	A	C	C	A	A	A
rubrivinctus	g	C	D	D	A	A	E	b	B	C	A	A	A	C	A	B	C	B	B	A
rufus A	F	C	D	aa	A	A	F	B	B	e	E	A	A	C	A	B	C	D	D	A
rufus B	F	C	D	aa	A	A	F	B	B	e	E	A	A	C	A	B	C	D	B	A
rufus C	F	C	D	aa	A	A	C	B	B	e	E	A	A	C	A	B	C	D	B	A
saxicola	O	C	D	t	A	G	f	B	C	C	G	F	C	D	A	B	C	A	A	A
semicinctus	X	C	D	j	A	C	p	A	Q	L	A	D	A	A	A	A	H	A	A	A
serrenoides A	D	C	D	D	B	C	f	B	P	C	A	A	A	D	A	B	C	B	D	A
serrenoides B	D	C	C	F	B	C	f	B	P	C	A	A	A	D	A	B	C	B	D	A
serriceps A	F	C	D	y	A	g	E	B	B	C	A	A	A	C	A	B	C	A	B	A
serriceps B	F	C	D	z	A	g	E	B	B	C	A	A	A	C	A	B	C	A	B	A
simulator	F	K	D	F	A	A	E	B	C	C	A	A	A	C	A	B	C	A	D	A
spinorbis	O	C	D	D	B	A	E	B	D	M	A	A	A	C	A	B	C	A	B	A
taczanowski A	P	A	D	W	A	I	R	H	C	I	A	A	A	A	A	D	C	B	A	C
taczanowski B	P	A	D	W	C	I	R	H	C	I	A	A	A	A	A	D	C	B	A	C
taczanowski C	P	A	D	W	C	I	R	H	C	I	A	A	A	A	A	D	C	A	A	C
thompsoni	O	H	D	Y	A	A	D	e	L	I	A	A	A	A	A	B	C	A	C	A
trivittatus A	F	A	D	V	A	F	K	E	C	H	A	A	A	A	A	E	B	B	A	C
trivittatus B	F	A	D	V	A	D	K	E	C	H	E	A	A	A	A	E	B	C	A	C
trivittatus C	F	A	D	V	B	D	K	E	B	H	E	A	A	A	A	E	B	C	A	C
trivittatus D	F	A	D	V	B	D	K	E	C	H	E	A	A	A	A	E	B	C	A	C
umbrosus	F	C	D	w	B	A	n	B	D	M	A	A	A	C	A	B	A	A	B	A
variegatus	F	C	D	E	A	A	D	B	B	C	A	A	A	B	A	B	C	A	C	A
vulpes A	B	D	D	V	A	A	h	B	C	G	A	C	A	A	A	E	B	B	A	B
vulpes B	B	D	D	V	A	A	h	B	C	H	A	C	A	A	A	E	B	B	A	B
vulpes C	B	D	D	i	A	A	h	B	C	H	A	C	A	A	A	E	B	B	A	B
wilsoni A	F	C	D	E	A	A	D	B	B	C	A	A	A	B	A	B	C	A	C	A
wilsoni B	F	C	A	i	A	A	D	B	B	C	A	A	A	B	A	B	C	A	C	A
zacentrus A	F	A	D	E	A	A	D	B	C	C	A	A	A	B	A	B	C	A	C	A
zacentrus B	F	A	D	A	A	A	D	B	C	C	A	A	A	B	A	B	C	A	C	A
zacentrus C	F	C	D	E	A	A	D	B	C	C	A	A	A	B	A	B	C	A	C	A
zacentrus D	F	A	D	E	A	A	D	B	C	B	A	A	A	B	A	B	C	A	C	A
Helicolenus hilgendorfi	J	G	F	Q	A	A	N	G	H	A	D	B	B	F	B	B	F	B	A	A
Sebastolobus alascanus A	H	E	E	O	A	H	M	F	G	F	C	B	B	E	A	D	E	B	E	B
Sebastolobus alascanus B	I	E	E	O	A	H	M	F	G	F	C	B	B	E	A	D	E	B	E	B
Sebastolobus alascanus C	H	F	E	O	A	H	M	F	G	E	C	B	B	E	A	D	E	B	E	B
Sebastolobus alascanus D	H	E	E	P	A	H	M	F	G	F	C	B	B	E	A	D	E	B	E	B

Identification key

Key for distinguishing *Sebastes* spp. using ND3/ND4 restriction site information. This is one of many possible schemes to identify unknown specimens to species level or to small groups of species. Because new intraspecific variation may be encountered, it is wise to confirm the identification by cutting the DNA using an additional one or two enzymes.

1. Digest mtDNA with *Mbo* I.
2. Place resulting restriction fragment patterns (haplotypes) in one of the following categories (see Appendices 1 and 2 for details).
   - a. O—*S. hubbsi* A, B, D.
   - b. P—*S. hubbsi* C.
   - c. A or B.
     Digest mtDNA with *Bst*N I.
     - i. B—*S. alutus*
     - ii. W—*S. elongatus* A
     - iii. E—*S. flavidus*
     - iv. F—*S. helvomaculatus*
     - v. C—*S. rastrelliger*
   - d. p or l.
     Digest mtDNA with *Bst*N I.
     - i. X—*S. semicinctus*
     - ii. F—*S. dalli*
   - e. R—*S. taczanowski*
   - f. q, V, C, J, f, j.
     Digest with *Bst*N I.
     - i. B—*S. levis*
     - ii. N—*S. nivosus*
     - iii. O.
       Digest mtDNA with *Bst*U I.
       1. B—*S. atrovirens*
       2. C—*S. saxicola*
     - iv. W—*S. elongatus*
     - v. g—*S. diploproa*
     - vi. F.
       Digest mtDNA with *Bst*U I.
       1. A—*S. paucispinis*
       2. C.
          Digest mtDNA with *Dde* I.
          - *a.* s—*S. pinniger*
          - *b.* aa—*S. rufus* C
       3. a—*S. carnatus*, *S. chrysomelas*
       4. B.
          Digest mtDNA with *Cfo* I.
          - *a.* D—*S. maliger*
          - *b.* C—*S. caurinus*
       5. G—*S. nebulosus*
     - vii. P—*S. macdonaldi*
   - g. D or e.
     Digest mtDNA with *Bst*N I.
     - i. F.
       Digest mtDNA with *Dde* I.
       1. A—*S. zacentrus* B
       2. E.
          Digest mtDNA with *Rsa* I.
          - *a.* C—*S. zacentrus* A,C,D
          - *b.* B—*S. emphaeus* B, *S. variegatus*, *S. wilsoni* A (identical)
          - *c.* D—*S. emphaeus* A
       3. cc—*S. inermis* C
       4. X or r.
          Digest mtDNA with *Bst*U I.
          - *a.* C—*S. miniatus*
          - *b.* H—*S. inermis* A
          - *c.* I—*S. inermis* B
       5. i—*S. wilsoni* B
     - ii. O.
       Digest mtDNA with *Dde* I.
       1. Y—*S. thompsoni*
       2. a—*S. joyneri*
   - h. c—*S. jordani* A
   - i. H—*S. babcocki* B
   - j. g—*S. hopkinsi* A
   - k. h—*S. vulpes*
   - l. E.
     Digest mtDNA with *Bst*N I.
     - i. B—*S. mystinus* A
     - ii. O—*S. spinorbis*
     - iii. D—*S. melanops*
     - iv. F or g.
       Digest mtDNA with *Dde* I.
       1. l.
          Digest mtDNA with *Bst*N I.
          - *a.* F—*S. entomelas*/*S. mystinus* A, C
          - *b.* B—*S. mystinus* B, D
       2. D—*S. rubrivinctus*
       3. G.
          Digest mtDNA with *Bst*U I.
          - *a.* C—*S. constellatus*
          - *b.* B—*S. chlorostictus*, *S. eos*, *S. rosenblatti* (identical)
       4. z—*S. serriceps* A
       5. k or y.
          Digest mtDNA with *Hin*d III.
          - *a.* A—*S. serriceps* B
          - *b.* B—*S. rosaceus*
   - m. G—*S. babcocki* A
   - n. K.
     Digest mtDNA with *Bst*N I.
     - i. Z—*S. hopkinsi* B
     - ii. O—*S. melanostomus*
     - iii. F.
       Digest mtDNA with *Hin*f I.
       1. A—*S. proriger*
       2. D—*S. trivittatus*
       3. E—*S. aleutianus* A
       4. B or F.
          Digest mtDNA with *Bst*U I.
          - *a.* A—*S. trivittatus*
          - *b.* C—*S. aleutianus* B
     - iv. G—*S. brevispinis*
   - o. a—*S. goodei*
   - p. F.
     Digest mtDNA with *Bst*N I.
     - i. A—*S. crameri*, *S. ciliatus*, *S. polyspinis* A, B (first 2 spp. and *S. polyspinis* A identical)
       Digest mtDNA with *Bst*U I.
       1. D—*S. crameri*, *S. ciliatus*, *S. polyspinis* A
       2. J—*S. polyspinis* B
     - ii. F.
       Digest mtDNA with *Dde* I.
       1. D—*S. borealis*
       2. aa—*S. rufus* A, B
     - iii. V—*S. polyspinis* C
   - q. d—*S. jordani* B
   - r. I—*S. ruberrimus*
   - s. i—*S. exsul*
   - t. b—*S. aurora*
   - u. k—*S. auriculatus*
   - v. r—*S. rcedi*

product with endonuclease *Bst*N I. Continue digesting with the specified restriction endonucleases, identifying the resultant haplotype, and continue to the next step until the species has been identified. Between one and five restriction enzymes will be needed to achieve the separation. Examining the fragment patterns of additional restriction enzymes can increase confidence in the identifications (see key).

Although variation observed in the 12S/16S region was not used in the key, it does provide alternatives to species identification that may be useful for resolving the identification of some species or for corroborating identifications, especially when there is intraspecific variation that has not been previously observed for the enzymes applied in resolving species. In particular, *Rsa* I, *Dde* I, and *Mbo* I exhibited substantial interspecific variation in the 12S/16S region. In addition, if one has reduced the possible species by other means, a single 12S/16S digest can be used in some instances. For example, *S. aleutianus* and *S. borealis* differ in fragments produced by *Bst*N I and by *Rsa* I, and *S. caurinus* and *S. maliger* also differ in fragments produced by *Rsa* I.

Discussion

Restriction site analysis of mtDNA is a simple and effective tool for identifying juveniles of *Sebastes* species. Because inexpensive equipment is used to obtain data from restriction fragment patterns, the analyses can be conducted in most laboratories, including many high school laboratories.

Although the restriction fragment key identified most (58 or 81.7%) of the 71 different rockfish species we evaluated, it failed to identify 13 species. The identities of those 13, however, were narrowed to five small groups of species. One group, *S. carnatus* and *S. chrysomelas*, are very closely related; they differ obviously only in body coloration as adults: *S. carnatus* has flesh-colored blotches on an olive-brown background, and *S. chrysomelas* has yellow blotches on a black background (Love et al., 2002). They are included in the subgenus *Pteropodus* (Kendall, 2000). Another group includes *S. chlorostictus*, *S. eos*, and *S. rosenblatti*, which are also morphologically similar, occur sympatrically, and are closely related (Chen, 1971; Love, 1996; Rocha-Olivares et al., 1999; Love et al., 2002); all are members of the subgenus *Sebastomus*. Estimates of divergence times of the subgenus *Sebastomus* suggest that the three species are the result of the most recent speciation events within the subgenus, which may have begun less than 140,000 years ago (Rocha-Olivares et al., 1999). Members of a third group, *S. emphaeus-S. variegatus-S. wilsoni*, are assigned to the subgenus *Allosebastes* (Kendall, 2000). The relationships between species in the other two unresolved groups are not as clear because the subgenera of the members differ. In one of those groups, *S. entomelas* is in subgenus *Acutomentum* and *S. mystinus* is in subgenus *Sebastosomus*. In the other subgroup, *S. polyspinis* remains unassigned to a subgenus, *S. crameri* is in *Eosebastes*, and *S. ciliatus* (subgenus *Sebastosomus*) has only recently been separated from *S. variabilis* (Orr and Blackburn, 2004). The similarities observed may actually reflect genetic relationships because the subgenera assignments are probably inaccurate reflections of phylogeny (Kendall, 2000). Our inability to resolve within those five groups of rockfish to species indicates the need for additional markers. Approaches for obtaining such markers include screening additional regions of the mtDNA and application of additional restriction enzymes. If additional mtDNA regions and restriction enzymes do not provide species-specific information, other molecular techniques such as microsatellites should be considered.

We applied the baseline data from which our key was developed to identification of recently extruded rockfish larvae in Southeast Alaskan waters (Gray et al., 2006). That application, which was made while the key presented in this article was being developed, evolved over subsequent years of application. The key was also used to delineate juvenile rockfishes from the southern California Bight (Li et al., in press). We were able to identify all the specimens to species or to narrow identification to one of the five small groups of genetically similar species. The identifications of juvenile rockfish were concordant with genetic and morphological criteria, except that the genetic key did resolve species in the closely related subgenus *Sebastomus*, which could not be resolved with morphological criteria. The larval specimens, in contrast, could not be identified to species with morphological criteria. We detected previously unobserved intraspecific variation in both studies as well. Neither the variation observed in the larval and juvenile studies, the intraspecific variation observed in developing the key, nor intraspecific variation observed among large numbers of individuals of several species examined as part of a population genetic analysis (Li, 2004) obscured species detection.

Molecular genetic keys can remove much of the guesswork for species determination in ichthyoplankton and juvenile surveys. Because DNA-based characters remain constant throughout the life of an individual, genetic divergence can provide unequivocal markers for species delineation. For specific questions involving the identification of small numbers of species, such as distinguishing between the two sibling species included in *S. aleutianus* (Gharrett et al., 2005), it is possible to develop assay methods (e.g., single nucleotide polymorphism—referred to as SNP (Collins et al., 1996), that can rapidly identify large numbers of specimens. Finally, such a key can be used to identify larval and juvenile species of *Sebastes* so that the variation in the morphological characters can be determined.

Acknowledgments

This work represents, in part, the master's thesis work of Z. Li at the University of Alaska Fairbanks. The project was supported by funding from the U.S. Geological

Survey (Biological Resources Division), Western Regional Office in Seattle, WA (R.W.O. 32) to AJG. AJG was at Hokkaido University and Kitasato University and was supported by the Japan Society for Promotion of Science when he contributed some of the effort to this study.

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Appendix 1

Restriction site locations for *Sebastes* spp., *Sebastolobus alascanus*, and *Helicolenus hilgendorfi* in the ND3/ND4 and 12S/16S mtDNA regions. Letters denote haplotypes (restriction digest patterns). "X" denotes presence of site, "O" denotes absence of site.

ND3/ND4 *Bst*N I sites	haplotypes																							
	A	B	C	D	E	F	G	H	I	J	L	M	N	O	P	V	W	X	Y	Z	a	b	c	g
112	O	X	X	X	X	X	X	X	X	X	O	X	X	X	X	O	O	X	X	O	X	X	X	X
291	O	O	O	O	X	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	X	X	O
551	O	O	O	O	O	O	O	X	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
829	X	X	O	X	X	X	X	X	X	X	X	X	X	X	X	X	X	O	O	O	O	X	X	X
1035	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1214	X	X	X	O	O	X	X	O	O	O	O	O	X	O	X	O	X	O	X	O	X	X	X	X
1261	O	O	O	O	O	O	O	O	X	O	X	X	X	O	O	O	O	O	O	O	O	O	O	O
1495	O	O	O	O	O	O	O	O	O	O	X	X	O	O	O	O	O	O	X	O	O	O	O	O
1694	O	O	X	X	X	X	X	O	O	O	O	O	O	X	X	O	X	X	O	X	O	O	X	X
1982	O	O	O	X	X	O	X	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O
2010	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
2121	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	X	O	O
2255	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
2325	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	O	X	O

ND3/ND4 *Bst*U I sites	haplotypes												
	A	B	C	D	E	F	G	H	I	J	K	a	b
4[1]	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)
344	O	O	O	O	O	X	O	O	O	O	O	O	O
668	O	O	O	O	O	O	O	X	O	O	O	O	O
710	O	O	O	O	O	O	O	O	X	O	O	O	X
1499	O	O	O	O	X	O	O	O	O	O	O	O	O
1854	O	O	O	X	O	O	O	O	O	X	X	O	O
2025	O	X	X	O	O	O	O	X	O	O	X	X	X
2109	O	O	O	O	O	O	O	O	X	X	O	X	O
2306	O	X	O	O	X	X	X	O	O	O	O	X	O

[1] The site at 4 is in the primer region.

Cfo I sites	haplotypes											
	A	B	C	D	E	F	I	J	K	a	b	g
709	X	O	X	X	X	X	X	X	X	X	X	X
1221	O	O	O	O	X	X	X	O	O	O	O	O
1436	O	O	O	O	X	O	O	O	O	O	O	O
1464	O	O	O	O	O	O	O	X	O	X	O	O
1472	O	O	O	O	O	O	O	O	O	O	X	X
1741	O	X	X	X	O	O	X	X	X	O	X	X
1762	O	O	O	O	O	O	O	O	X	O	O	O
1813	O	O	X	O	O	O	O	O	O	O	X	O

ND3/ND4 *Dde* I sites	haplotypes																							
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	
65	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	
195	X	O	O	X	X	X	X	X	X	X	X	X	X	X	O	O	O	O	O	O	X	X	O	
266	O	O	O	O	O	O	X	O	X	O	O	X	O	O	X	X	X	O	O	O	O	O	O	
298	X	X	O	X	X	X	X	O	X	X	X	X	X	X	O	O	X	O	O	O	O	X	X	
336	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
374	X	X	X	O	X	O	O	O	O	X	O	O	X	O	O	O	O	X	X	X	O	X	O	

continued

Appendix 1 (continued)

ND3/ND4 (continued) *Dde* I sites	haplotypes																					
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
590	O	X	X	X	X	X	X	X	X	X	X	X	X	X	O	O	X	X	X	X	X	X	X
624	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
663	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O
695	O	O	O	O	O	O	O	O	X	O	O	X	O	O	O	O	O	O	O	O	O	O	O
754	O	O	O	O	O	O	O	O	X	O	O	X	X	O	O	O	X	O	O	O	X	X	X
1144	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1190	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	X	X	O	O	O
1257	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O
1409	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O
1560	O	O	O	O	O	O	O	O	X	O	O	X	O	O	O	O	O	X	O	O	O	O	O
1577	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	X	X	O	O	O	O	O	O
1587	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1601	X	O	X	X	X	X	X	X	X	X	X	X	X	X	O	O	O	X	X	X	X	X	X
1696	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O
1722	O	O	O	O	O	O	O	O	O	X	O	O	O	X	X	X	X	O	O	O	O	O	O
1779	O	O	X	O	O	O	O	O	X	O	O	X	X	O	O	O	O	X	X	X	O	O	X
1795	O	O	O	O	O	X	X	X	X	X	X	X	X	O	O	O	X	O	O	O	X	X	X
1912	X	X	X	X	X	X	X	X	O	X	X	X	X	X	O	O	X	X	X	O	X	X	X
2091	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	X	O	O
2122	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
2188	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	X	O	O	O	O	O	O	O
2374[2]	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)

ND3/ND4 *Dde* I sites	haplotypes (continued)																						
	X	Y	Z	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t
65	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
195	O	O	X	X	O	X	X	O	X	X	X	X	X	X	X	X	X	X	O	X	X	X	X
266	O	O	X	O	X	O	O	O	O	O	O	O	X	O	O	O	O	O	X	O	O	O	X
298	X	O	X	O	X	X	X	X	X	X	O	X	X	X	O	X	X	X	X	X	O	X	O
336	X	O	X	O	X	X	X	X	X	X	X	X	X	X	O	X	O	O	X	X	X	X	X
374	X	X	O	X	O	O	O	X	X	X	O	X	O	O	O	O	O	O	O	O	X	X	O
590	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
624	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
663	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
695	O	O	X	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
754	X	O	X	O	O	X	O	O	X	O	O	X	O	X	O	X	X	X	O	X	O	O	O
1144	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O
1190	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1257	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1409	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1560	X	X	X	X	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1577	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1587	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O
1601	X	X	X	X	X	O	X	O	X	X	X	X	O	X	X	X	X	X	O	O	X	X	X
1696	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1722	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1779	X	X	X	X	X	O	O	O	X	O	X	O	X	O	O	O	O	O	O	O	O	O	X
1795	X	X	X	X	X	X	X	X	X	X	X	O	X	O	X	X	O	X	X	X	X	X	X
1912	X	X	X	X	O	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
2091	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
2122	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
2188	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
2374[2]	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)

continued

Appendix 1 (continued)

ND3/ND4 *Dde* I sites	haplotypes (continued)									Hind II sites	haplotypes						
	u	v	w	x	y	z	aa	bb	cc		A	B	C	E	F	b	g
65	O	O	O	O	O	O	O	O	O	308	O	O	O	O	O	O	X
195	X	X	X	O	X	X	X	X	X	320	O	O	O	O	X	O	O
266	O	X	O	O	O	O	O	X	O	324	O	O	O	O	O	X	O
298	X	X	X	O	X	X	X	X	O	978	O	O	O	O	O	X	O
336	O	X	X	X	X	X	X	X	O	1007	O	X	O	O	X	O	O
374	O	O	O	O	O	O	O	O	X	1071	O	O	O	X	O	O	O
590	O	X	X	X	X	X	X	X	X	1091	O	O	X	O	O	O	O
624	O	O	O	X	O	O	O	O	O								
663	O	O	O	O	O	O	O	O	O								
695	O	X	O	O	O	O	O	X	O								
754	X	O	O	O	O	O	X	O	O								
1144	O	O	O	O	O	O	O	O	O								
1190	O	O	O	O	O	O	O	O	O								
1257	O	O	O	O	O	O	O	O	O								
1409	O	O	O	O	X	X	O	O	O								
1560	O	X	O	O	O	O	O	O	O								
1577	O	O	O	O	O	O	O	O	O								
1587	O	O	O	O	O	O	O	O	O								
1601	X	X	O	X	X	O	X	X	X								
1696	O	O	O	O	O	O	O	O	O								
1722	O	O	O	O	O	O	O	O	O								
1779	O	X	O	O	O	O	X	X	X								
1795	X	X	X	X	O	O	X	X	X								
1912	X	X	X	X	X	X	X	X	X								
2091	O	O	O	O	O	O	O	O	O								
2122	O	O	O	O	O	O	O	O	O								
2188	O	O	O	O	O	O	O	O	O								
2374[2]	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)	(X)								

[2] The site at 2374 is in the primer region.

ND3/ND4 *Hinf* I sites	haplotypes															
	A	B	C	D	E	F	G	H	I	N	O	P	Q	a	b	g
43	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O
130	O	X	O	O	O	X	O	O	X	O	X	X	O	O	O	O
183	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O
389	O	X	X	O	O	O	O	X	O	O	O	O	O	O	O	O
472	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X
494	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
621	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O
853	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O
999	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O
1017	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O
1342	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O
1448	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O
1537	O	O	O	O	O	O	X	O	O	O	X	O	O	X	O	O
1755	O	O	O	O	X	X	O	O	O	O	O	O	O	O	O	O
1888	O	O	O	X	O	O	O	X	O	O	O	O	O	O	O	O
2011	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O
2232	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

continued

Appendix 1 (continued)

ND3/ND4 *Mbo* I sites	haplotypes																					
	A	B	C	D	E	F	G	H	I	J	K	M	N	O	P	R	V	a	b	c	d	e
150	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
190	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
198	X	X	X	X	X	X	X	X	X	X	X	O	O	X	X	X	X	X	X	X	X	X
261	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
272	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O
302	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	X	O	O	O	O
632	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X
648	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
758	X	X	X	X	X	X	X	O	X	X	X	X	O	O	O	O	O	X	X	X	X	X
797	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O
861	O	O	O	O	O	O	X	X	O	O	O	O	O	O	O	O	O	O	O	X	X	O
886	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
900	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O
940	X	X	X	X	X	X	X	X	X	X	X	X	X	O	O	X	X	X	X	X	X	X
971	O	X	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1029	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O
1270	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O
1481	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	X	O
1534	O	O	O	O	X	X	X	X	X	O	X	X	X	O	X	O	X	X	X	X	X	O
1647	O	O	X	X	O	X	O	O	X	X	X	O	X	X	X	X	X	O	X	X	X	X
1658	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1748	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
1979	X	X	X	X	X	X	X	X	X	X	X	O	X	X	X	X	X	X	X	O	X	X
2016	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O
2339	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O

ND3/ND4 *Mbo* I sites	haplotypes (continued)											
	f	g	h	i	j	k	l	m	n	p	q	r
150	O	O	X	O	O	O	O	O	O	O	O	O
190	O	O	O	O	X	O	O	O	O	O	O	O
198	X	X	O	X	X	X	X	O	X	X	X	X
261	O	O	O	O	O	O	O	O	X	O	O	O
272	O	O	O	O	O	O	O	O	O	O	O	O
302	O	O	O	O	O	O	O	O	O	O	O	O
632	O	O	O	O	O	O	O	O	O	O	O	O
648	O	O	O	O	O	O	O	O	O	O	O	O
758	X	X	X	X	X	X	X	X	X	X	X	X
797	O	O	O	O	O	O	O	O	O	O	O	O
861	O	O	O	O	O	O	O	O	O	O	O	O
886	O	O	O	O	O	O	O	O	O	O	O	O
900	O	O	O	O	O	O	O	O	O	O	O	O
940	X	X	X	X	X	X	O	X	X	O	O	X
971	O	O	O	O	O	O	O	O	O	O	O	X
1029	O	O	O	O	O	O	O	O	O	O	O	O
1270	O	O	O	X	O	X	O	O	O	O	O	O
1481	O	O	O	O	O	O	O	O	O	O	O	O
1534	O	X	X	X	O	O	O	X	X	O	X	X
1647	X	X	X	O	X	X	X	X	O	X	X	X
1658	X	O	O	O	O	O	O	O	O	O	O	O
1748	O	O	O	O	O	O	X	O	O	O	O	O
1979	X	O	X	X	X	X	X	X	X	X	X	X
2016	O	O	O	O	O	O	O	O	O	O	O	O
2339	O	O	O	O	O	O	O	O	O	O	O	X

continued

Appendix 1 (continued)

ND3/ND4 *Msp* I sites	haplotypes															
	A	B	C	D	E	F	G	H	L	M	a	b	d	e	g	
30	X	X	X	X	X	X	X	X	X	O	X	X	X	X	X	
933	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	
1199	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	
1230	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	
1261	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	
1541	O	O	O	O	O	O	O	X	O	O	O	X	O	O	X	
1624	O	O	O	O	O	O	O	O	X	O	O	O	O	X	O	
1738	X	X	X	X	X	X	X	O	X	X	X	X	X	X	X	
1826	X	X	O	X	X	O	O	X	X	X	O	X	X	X	X	
1844	O	O	O	X	X	O	O	O	O	O	O	O	X	O	O	
2073	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	
2110	O	X	X	O	X	O	O	O	O	O	O	O	X	X	X	

Rsa I sites	haplotypes																	
	A	B	C	D	E	F	G	H	I	J	L	N	O	P	Q	R	a	b
346	O	O	O	X	X	O	X	X	O	O	X	X	O	X	O	O	O	O
561	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O
742	O	O	O	O	O	O	O	X	X	O	O	O	O	O	O	O	O	O
1077	O	O	O	O	O	X	O	O	O	O	X	X	O	O	O	O	O	O
1231	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O
1321	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O
1339	O	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O
1357	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O
1433	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O
1492	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O
1863	O	O	X	O	X	O	O	X	X	X	X	O	O	O	O	O	O	X
1985	O	X	X	X	X	X	X	X	X	X	X	X	X	O	X	X	X	O
2063	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X	O	O	O

ND3/ND4 *Sty* I sites	haplotypes																
	A	B	C	D	E	F	G	H	I	L	M	N	O	b	d	e	g
49	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
108	O	O	O	O	O	O	O	O	O	O	X	O	O	X	O	O	X
194	O	O	O	X	X	X	O	O	X	O	O	X	O	X	O	O	O
365	X	X	X	X	O	O	X	X	X	X	X	X	O	X	O	X	X
391	O	O	O	O	X	X	O	O	O	X	O	O	O	O	O	O	O
534	X	O	X	X	X	X	O	O	X	X	X	X	X	X	O	X	X
1258	O	O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O
1570	O	X	X	X	X	X	O	O	O	X	X	O	X	O	X	X	O
1725	O	O	O	O	O	O	X	O	O	O	O	X	O	O	O	X	O
2311	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

12S/16S *Bst*N I sites	haplotypes						
	A	B	C	D	E	F	G
326	X	X	X	X	O	X	X
988	O	O	O	X	O	X	O
1105	O	O	O	O	O	X	O
1530	O	O	O	O	O	O	X
1687	O	O	X	O	O	O	O
1741	O	X	O	O	O	O	O
2416	X	X	X	X	X	X	X

Appendix 1 (continued)

12S/16S *Bst*U I sites	haplotypes A	B	C	D	E	F
87	X	X	X	X	X	X
600	X	O	X	X	O	X
664	X	X	X	X	X	X
729	X	X	O	O	X	X
1633	O	O	O	O	X	O
1872	X	X	X	X	X	X
2128	X	X	X	X	X	X
2191	O	O	O	X	O	X

Cfo I sites	haplotypes A	B	C	D
537	X	X	O	X
602	X	O	X	X
665	X	X	X	X
1630	O	O	O	X
1898	X	X	X	X
2268	X	X	X	X

Dde I sites	haplotypes A	B	C	D	E	F	G	H	I
44	X	X	X	X	X	X	X	X	X
55	X	X	X	X	X	X	X	X	X
976	X	X	X	X	X	O	O	O	X
1043	X	X	O	X	X	O	O	O	X
1056	X	X	O	X	O	O	X	O	X
1304	X	X	X	X	X	O	X	X	X
1339	O	O	O	O	O	O	O	O	X
1735	O	X	X	X	X	O	X	X	X
2181	X	O	X	X	X	O	O	X	X
2393	X	X	X	X	X	X	X	X	X

Hinf I sites	haplotypes A	B	C	D	E	G	H	I
982	O	O	X	O	O	O	O	X
1181	O	O	O	O	O	X	O	O
1291	X	X	X	O	O	X	X	X
1700	O	O	O	O	O	O	X	X
2094	O	X	X	O	X	O	X	X

Hind II sites	haplotypes A	B
1717	X	O

12S/16S *Mbo* I sites	haplotypes A	B	C	E	F	G	H	I
201	O	X	X	O	O	X	X	X
849	X	X	X	O	X	X	X	X
1015	X	X	X	X	O	O	X	X
1210	O	O	O	O	O	O	O	X
1403	X	X	X	X	X	X	X	X
1507	X	O	X	X	X	X	X	X
1637	O	O	O	O	O	O	X	O
1984	X	X	X	X	X	X	X	X
2059	X	X	X	X	X	X	X	X
2228	X	X	X	X	X	X	X	X
2318	X	X	X	X	X	X	X	X
2388	X	X	X	X	X	X	X	X

Msp I sites	haplotypes A	B	C	D	E	F
65	X	X	X	X	X	X
241	O	O	O	O	O	X
330	O	O	X	X	O	O
766	X	X	X	X	X	X
1259	O	X	X	O	O	X
1390	X	X	X	X	X	X
1535	X	X	X	X	O	X
2226	X	X	X	X	X	X
2403	X	X	X	X	X	X

Rsa I sites	haplotypes A	B	C	D	E
293	O	O	O	O	X
507	O	O	X	X	O
588	O	O	O	O	X
761	X	X	X	X	X
950	O	O	O	O	X
1000	X	X	X	X	O
1071	X	X	X	X	O
1263	O	O	O	O	X
1308	O	X	O	X	X
1358	X	X	X	X	X
2164	O	O	O	O	X

Sty I sites	haplotypes A	B	C	D
295	X	O	X	X
982	O	O	O	X
1748	O	O	X	O
2053	O	X	O	O
2254	X	X	X	X

Variation in yellowfin tuna (*Thunnus albacares*) catches related to El Niño-Southern Oscillation events at the entrance to the Gulf of California

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Abstract—Fishery catch data on yellowfin tuna (*Thunnus albacares*) were examined to study the effects of El Niño events between 1990 and 1999 for an area in the northeastern tropical Pacific (18–24° N, 112–104° W). The data were extracted from a database of logbook records from the Mexican tuna purse-seine fleet. Latitudinal distribution of the catches increased from south to north for the 10-year period. Highest catches and effort were concentrated between 22°N and 23°N. This area accumulated 48% of the total catch over the 10-year period. It was strongly correlated with El Niño-Southern Oscillation (ENSO) events. At least two periods of exceptionally high catches occurred following El Niño events in 1991 and 1997. Peaks of catches were triggered by the arrival of positive anomalies of sea surface temperature (SST) to the area. A delay of two to four months was observed between the occurrence of maximum SST anomalies at the equator and peaks of catch. Prior to these two events, negative SST anomalies were the dominant feature in the study area and catch was extremely low. This trend of negative SST anomalies with low catches followed by positive SST anomalies and high catches may be attributed to northward yellowfin tuna migration patterns driven by El Niño forcing, a result that contrasts with the known behavior of decreasing relative abundance of these tuna after El Niño events in the eastern Pacific. However, this decrease in relative abundance may be the result of a local or subregional effect.

Manuscript submitted 3 December 2003 to the Scientific Editor's Office.
Manuscript approved for publication 9 August 2005 by the Scientific Editor.
Fish. Bull. 104:197–203 (2006).

The entrance to the Gulf of California (from 18°N to 24°N and 104°W to 112°W) is located in the convergence zone of the North Pacific Gyre, where the California Current separates from the coast to feed the North Equatorial Current. It has a complex hydrographic structure due to the confluence of different water masses (Roden and Groves, 1959; Roden, 1972; Álvarez-Borrego and Schwartzlose, 1979; Bray and Robles, 1991; Torres-Orozco, 1993). This region is highly responsive to the El Niño phenomenon. Its main response is characterized by positive sea level anomalies, warming of the upper layer, and a general alteration of water current patterns (Baumgartner and Christensen, 1985; Robles and Marinone, 1987; Torres-Orozco, 1993; Lavín et al., 1997; Ortega-García et al., 1999; Trasviña et al., 1999; Castro et al., 2000; Bernal et al., 2001).

High abundance of yellowfin tuna (*Thunnus albacares*; YFT) is reported in the study area (Allen and Punsly, 1984; Castro-Ortiz and Quiñones-Velásquez, 1987; Muhlia-Melo, 1993; Ortega-Garcia, 1998). However, studies about the YFT interaction with the physical environment of the Mexican Pacific are lacking. Blackburn (1965, 1969) considers that the abundance of the YFT correlates with sea surface temperature (SST) in the range of 20°C to 30°C, but it can also be present in regions having temperatures between 18°C and 31°C. Blackburn (1969) considered 30°C as an optimal estimate of the maximum temperature of occurrence of YFT. Similarly, Ortega-García (1998) reported that YFT are distributed in regions where SST ranges from 17°C to 31°C and that they are frequently observed in waters close to 28°C. Other studies such as that of Laevastu and Rosa (1963) and Castro-Ortiz and Quiñones-Velasquez (1987) have indicated that YFT are found at concentrations favorable to commercial fisheries in regions where the SST ranges from 20°C to 28°C. In summary, YFT catches are historically reported to

occur at SST values ranging from 12° to 30°C, and favorable catches are reported between 17° and 25°C (Lehodey[1]). More recently, Bautista-Cortes (1997) has studied the relationships between varying vertical temperature structure and YFT catches in the Mexican Pacific to 140° longitude W, finding that the depth of the 23°C isotherm is related to catch and that the shallower the isotherm, the larger the tuna catches.

Castro-Ortiz and Quiñones-Velasquez (1987) reported reduced catches of YFT during the 1982–83 El Niño events in the northeastern Pacific, in contrast to the following 1984–85 seasons. The 1982–83 El Niño event was reported to have caused the largest decrease in the availability-vulnerability index ($AVI=CPUE/(1-SSR)$; where SSR is the successful-set ratio and $CPUE$ is catch per unit of effort; IATTC[2]). This finding is consistent with the resource being less susceptible to fishing in the northeastern Pacific during an intense El Niño. Lehodey[1] analyzed data of purse-seine and longline CPUE of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albcares*), bigeye (*Thunnus obesus*), and albacore (*Thunnus alalunga*) tunas during El Niño and La Niña events, from 1982 to 1998 for the whole tropical Pacific Ocean (20°S to 20°N). He concluded and supports the hypothesis that ENSO affects the recruitment of skipjack, yellowfin, and bigeye tunas positively in the western Pacific. A direct positive effect related to the vertical change in the thermal structure during El Niño increased purse-seine catches of yellowfin in the western Pacific. He suggested two theoretical cases be considered for yellowfin and bigeye in the eastern Pacific: either a positive La Niña effect on the recruitment and catchability, or conversely a positive El Niño effect on recruitment and catchability. His statistical analysis did not identify the direct effects of ENSO on catchability for yellowfin and bigeye tunas. He suggested the need for additional analyses in the eastern Pacific region and for comparisons with independent results from modeling and observations to confirm the preliminary results. Lu et al. (2001) analyzed catches of YFT and bigeye tuna caught by the longline fleet of the tropical Pacific Ocean. They concluded that high hook rates for both species were mostly associated with regions where SST increased during El Niño or La Niña years. During La Niña episodes, YFT populations appear to undergo a poleward displacement thus shifting both north and south of the equator. During El Niño events YFT populations in the equatorial Pacific are found where SST anomalies are higher, in the central and eastern equatorial Pacific.

For the region of interest, Ortega-García et al. (1999) studied the impact of the ENSO during the 1997–98 El Niño events in comparison to the 1996–97 non El Niño year within the eastern Pacific Mexican purse-seine tuna fishery. They reported that during the first months of the ENSO (July–December 1997) of the El Niño event, the extent of the YFT catches was higher in oceanic waters than the observed catches during a non El Niño year in these areas for the same period. A decline of effort was observed along the coast of Baja California and inside the Gulf of California. In contrast, during the second part of the ENSO El Niño 1997–98 (January–June 1998), an increase of effort was observed along the coasts of Baja California and inside the Gulf of California; however, a decrease of effort was observed in oceanic areas.

The relative abundance of YFT in the eastern Pacific is reported to diminish during El Niño events; however, as supported by the IATTC[2] report, the YFT vertical displacement during El Niño events generates a diminishing fishing effort for the purse-seine fleet in traditional catch areas. As a consequence, this has led to a good recruitment and greater yield-per-recruitment. Large recruitments after El Niño events are reported to occur in the eastern Pacific. Joseph and Miller[3] analyzed YFT catch data from the eastern Pacific for a 22-year period and found positive anomalies in tuna recruitment after El Niño events. Large recruitments were observed in years 1971, 1974, 1978 and 1985, all of which were preceded by the El Niño events of 1969, 1972, 1976, and 1983, respectively.

The objective of the present study was to examine the effect of the ENSO El Niño and La Niña events for a 10-year period (1990–99) on YFT catches in the entrance to the Gulf of California, an area of importance for the industry and for the ecology of the resource in the eastern Pacific.

Materials and methods

The classification of El Niño intensities was taken from the Climate Prediction Center (NOAA[4]). The process of classification takes into account re-analyzed SSTs produced at the National Centers for Environmental Prediction (NCEP), at the Climate Prediction Center, and at the United Kingdom Meteorological Office.

Environmental data in the form of monthly means of sea surface temperature anomalies (SSTAs) from 1990 to 1999 were extracted from the NCEP monthly SSTA data-

[1] Lehodey, P. 2000. Impacts of the El Niño Southern Oscillation on tuna populations and fisheries in the tropical Pacific Ocean. Working Paper. RG-1, 32 p. Oceanic Fisheries Programme, Noumea, New Caledonia, Secretariat of the Pacific Community. http://www.spc.org.nc/OceanFish/Html/SCTB/SCTB13/rg1.pdf [accessed on 20 February 2002].

[2] IATTC (Inter American Tropical Tuna Commission). 1989. Annual Report of the Inter-American Tropical Tuna Commission, 1988. Annu. Rep. IATTC, 288 p. http://www.iattc.org/PublicationsSPN.htm [accessed on 11 March 2002].

[3] Joseph, J., and F. R. Miller. 1988. El Niño and the surface fishery for tunas in the eastern Pacific. *In* Proceedings of tuna fish. res. conf., p. 199–207. Japan Fish. Agency-Far Seas Fish. Res. Lab. Muguro Gyogyo Kyogikai Gjiroku, Suisancho-Enyo Suisan Kenkyusho.

[4] NOAA (National Oceanic and Atmospheric Administration). 2001. Cold and warm episodes by season. Website: http://www.cpc.ncep.noaa gov/products/analysis_monitoring/ensostuff/ensoyears.html [accessed on 10 January 2002].

base (IRI[5]). The SST fields were blended from ship, buoy, and bias-corrected satellite data. A description of this procedure can be found in Reynolds and Smith (1994). SSTA data for El Niño region 3 (NIÑO3, from 150°W to 90°W and from 5°N to 5°S) were obtained from Climate Prediction Center databases (CPC[6]).

Yellowfin tuna catch data were obtained from the database of the ATUN (tuna) Project of CICIMAR (the Interdisciplinary Research Center of Marine Science of the National Polytechnic Institute in La Paz, Mexico). This database has information on daily fishing activities for about 80% of the Mexican purse-seine fleet operating in the eastern Pacific. The data used in the present study include carrying capacity, catch-by-species, location, and school type (YFT associated with dolphins; YFT associated with floating objects; and free-swimming YFT), from 1990 to 1999, comprising 11,690 records. Total distribution of the sets made by the Mexican purse-seine fleet from 1990 to 1999 at the entrance of the Gulf of California is shown in Figure 1.

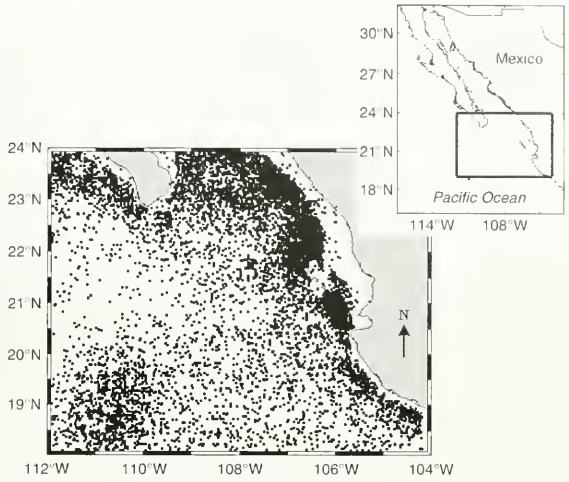

Figure 1

Total distribution of the sets made by the Mexican purse-seine fleet during 1990 to 1999 at the entrance to the Gulf of California. Catch data for yellowfin tuna (*Thunnus albacares*) were obtained from the CICIMAR (the Interdisciplinary Research Center of Marine Science of the National Polytechnic Institute in La Paz, Mexico).

Interannual variation

In order to study annual variation, total catches of YFT of the purse-seine fleet within the study area were accumulated by year. A cross-correlation analysis was applied to obtain information on lags between SST anomalies and YFT catches.

Latitudinal stratification

In order to analyze the latitudinal catch variation of YFT within the study area, catch data for the period 1990–99 were accumulated in six latitudinal bands of one degree from 18°N to 24°N at the entrance of the Gulf of California. Longitudinal limits extended from the coastal line of the Mexican continent (from 104°W to 112°W).

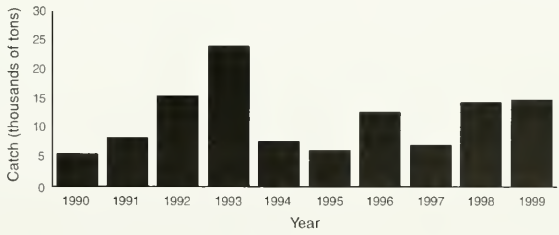

Figure 2

Total catch for yellowfin tuna (*Thunnus albacares*) by year during 1990–99 in the study area.

Results

Interannual variation in YFT catch

The catch of YFT in the study area showed high interannual variation (Fig. 2). This high variation showed substantial increments, 85% from 1991 to 1992, 54% from 1992 to 1993, 102% from 1995 to 1996, and 102% from 1997 to 1998. In particular, the sum of the two El Niño years in the record (1991–93, 1997–98) represents 59.5% of the total catches over the 10-year period.

Latitudinal variation in YFT catches

Figure 3 shows the variation of catch and effort (in sets) from 1990 to 1999. Vertical bars include catches from different one-degree latitudinal range areas between 18°N and 24°N and meridional ranges between 104°W to 112°W (Fig. 1). With the exception of the southern 18–20°N area,

[5] IRI (International Research Institute for climate prediction). 2002. Sea surface temperature anomaly data. Website: http://ingrid.ldgo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv1/.monthly/.ssta/ [accessed on 9 February 2002].

[6] CPC (Climate Prediction Center). 2002. Monthly atmospheric and SST indices. Website: http://www.cpc.ncep.noaa.gov/data/indices/index.html [accessed on 9 February 2002].

there is a general linear increase of catch with latitude. Fishing effort was concentrated in the 22–23°N and 23–24°N areas. Both account for 48% of the total capture for the 10-year period in this region. From 18° to 21°N, catch values averaged 12.9% of the total catch.

Yellowfin tuna catches affected by ENSO events

Sea surface temperature anomalies (SSTA) were used to investigate the effect of interannual warming or cooling events on the variability of YFT catch. Anomalies for

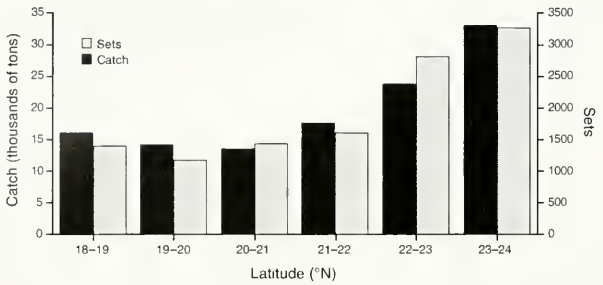

Figure 3

Latitudinal distribution of catches of yellowfin tuna (*Thunnus albacares*) for the period 1990–99.

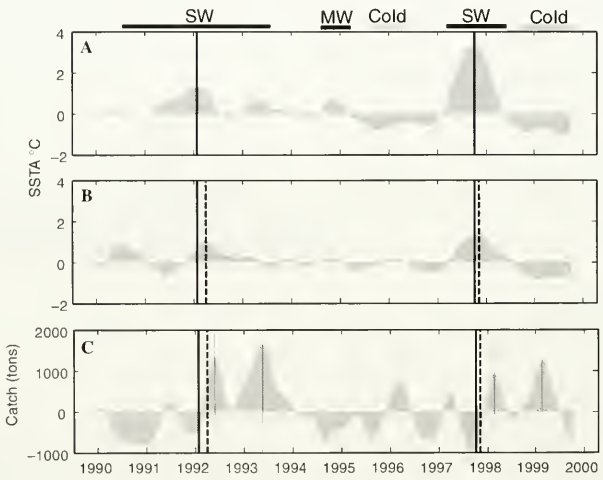

Figure 4

Sea surface temperature anomalies (SSTAs) in the El Niño region 3 (**A**), SSTAs in the study area (**B**) and catches of yellowfin tuna (*Thunnus albacares*) (**C**). Bars at the top show the equatorial central Pacific episodes as compiled by the Climate Prediction Center (see "Methods" section): Strong warm (SW) peaks of catch are indicated by thin vertical lines. Thick vertical lines indicate maximum SST anomalies in NIÑO3 (A). Dashed vertical lines indicate peaks of SSTA in the area of study (B). Moderate warm (MW) and cold episode. The maximum intensity of the warm episodes is marked with dashed lines (B and C).

the entrance to the Gulf of California were calculated between 22°N and 23°N and 103°W to 112°W. These anomalies were extracted from the Reynolds and Smith (1994) monthly 1-degree SSTA climatology. This variable was then compared to the catch of YFT. We did not examine SSTAs south of 21°N because they fall within the Mexican Warm Pool (Trasviña et al., 1999), where persistently high SSTs (above 27°C all year in the warm pool region) mask the propagation of warm and cold signals from the Equator. The 10-year time series (1990 to 1999) was "detrended" and filtered to eliminate periods shorter than three months, as described in Godin (1972).

SSTAs in the NIÑO3 (Fig. 4A) showed cold and warm conditions associated with five identifiable events. These events were the following: 1) warm El Niño events in 1991–92 (strong warm, SW), 2) in 1994–95 (moderate warm, MW), and 3) in 1997–98 (strong warm, SW); 4) moderately cold La Niña events that took place in 1995–96 and 5) in 1998–99. Strong warm events are marked with a black line located at each respective maximum SSTA (Fig. 4). The 1997–98 was the strongest warm episode in the 1990–99 decade.

The 1991–92 and 1997–98 SSTAs in El Niño region 3 were higher, by more than 1°C, than the SSTAs in the study area (Fig. 4, A and B). Within the 10-year period, near-normal conditions occurred from 1993 to 1996. The coldest and most persistent event of this decade took place in the study area from July 1998 to December 1999, i.e., during a moderate La Niña event.

Significant interannual variability of YFT catches was observed during the 10-year period in the study area (Fig. 4C). This graph shows the time series of monthly values of YFT catch anomalies related to the average for the 10-year period. Five exceptionally high catch events in years 1992, 1993, 1996, 1998, and 1999 were observed. These years account for 70% of the total capture during the 10-year period.

Several qualitative and quantitative features were apparent from these results:

1 Catch peaks in 1992 and 1998 occurred 3 (r=0.73) and 4 (r=0.64) months, respectively, after the onset of an El Niño event at the equator (time span between thin and thick lines) (Fig. 4, A and C).
2 High catches of YFT at the entrance of the Gulf of California in 1992 and 1998 occurred 2 (r=0.71) and 3 (r=0.73) months, respectively, after the SST anomaly signal reached the study area (time span between dashed and thin lines) (Fig. 4, B and C).
3 Higher catches of YFT occurred during the spring following an El Niño winter. These were observed in the spring of 1992 and 1998 (thin lines; Fig. 4C).
4 Peaks of YFT catch were also observed in 1993 and 1999. These occurred one year after the El Niño event. The 1993 peak took place in nearly normal SST conditions, whereas the 1999 peak occurred during negative SST anomalies (La Niña event, Fig. 4, B and C). These peaks of YFT catch were higher than the ones recorded in the previous year during the El Niño event 1991–92 and during 1997–98.

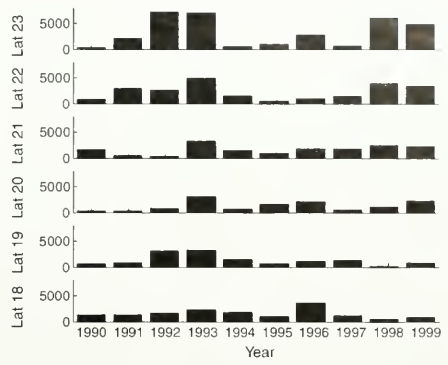

Figure 5

Annual catches (in tons) of yellowfin tuna (*Thunnus albacares*) in latitudinal bands within the area of study for the period 1990–99.

5 The 1996 peak seemed not to be related to the variability of SST anomalies alone.
6 There was a delay from one to two months between the mature phase of the El Niño event at the equator and the presence of high SSTAs in the study area (time span between thick and dashed lines in Fig. 4, A and B).

Annual YFT catches of stratified latitudinal bands within the study area are shown in Figure 5. A progressive increase in YFT catches from southern to northern latitudes was observed in years 1993 and 1999. This progressive increase may be indicative of a northward movement of the resource. This phenomenon has been observed in the western tropical Pacific Ocean during La Niña events where YFT have dominated the longline catch (Lu et al., 2001).

Discussion

Catch affected by the onset El Niño

Cross-correlation between the onset of El Niño at the equator in 1991–92 and 1997–98 with catch peaks of YFT in the study area showed a delay of three and four months respectively. Catch peaks of YFT at the entrance of the Gulf of California in 1992 and 1998 occurred two to three months after the SSTA signal reached the study area. These results are similar to those found by Lehodey[1] in the western and central regions of the Pacific Ocean, where rising (deepening) of the mixed-layer depth related to El Niño (La Niña) was associated with an increase in the pole-and-line and purse-seine CPUE of YFT and where there

was a concomitant delay of two to three months in this increase.

Catch of YFT in relation to recruitment

Recruitment explains most of the YFT catch fluctuations in relation to El Niño events at the entrance of the Gulf of California. A recurrent pattern in the time-series of the catch revealed a peak of catch fourteen (1993) to twelve (1999) months following an El Niño event. A similar result has been observed in a cross-correlation between the Southern Oscillation index (SOI) and the long-line series of catch data for yellowfin tuna; a positive correlation was found in the eastern Pacific region after a lag of fourteen months (Lehodey[1]). This finding supports the hypothesis of a recruitment base (age-effect) for yellowfin because at 14 months YFT reach 75 cm, corresponding to the first age class recruited to the long-line fishery. These results are also consistent with those from previous analyses of time-series of catches of YFT in the eastern Pacific, namely by Joseph and Miller[3] and the IATTC[2]. Therefore, recruitment can be the major explanation of the YFT catch fluctuations in relation to El Niño events at the entrance of the Gulf of California.

Catch distribution of YFT related to ENSO episodes

For the long-line fishery in the tropical Pacific Ocean, areas with significant higher hook rates of YFT during El Niño years are located east of 150°W within tropical waters of the central eastern Pacific (Lu et al., 2001). Conversely, higher hook rates occur during La Niña episodes in areas where SSTs rise during El Niño events. These two findings may provide two possible reasons for the change in hook rates: the expansion of optimal habitat and the change in vulnerability of the resource to the fishing gear during the ENSO episodes.

Conclusions

At the entrance of the Gulf of California, an El Niño event is associated with an increase in the purse-seine catch of YFT after two to three months, when SSTAs reach the study area. Similarly, this increase is delayed three to four months after the onset of El Niño at the equator.

A positive correlation of El Niño on YFT catch at the entrance of the Gulf of California after a twelve to fourteen month delay supports the hypothesis that the ENSO affects recruitment of YFT. This correlation seems to be independent of the thermal structure during the recruitment phase. In 1993, normal conditions in SST were present, whileas in 1999 La Niña was observed.

A northward displacement of YFT seems to occur at the entrance of the Gulf of California twelve to fourteen months after El Niño events. Lower catches in southern latitudes were recorded, whereas higher catches were recorded in northern latitudes. Similar results have been observed in the central Western Pacific for the long-line fishery (Lu et al., 2001).

Forecasting catch within the study area may give us the ability to reliably develop predictions of catch following El Niño or La Niña events.

Acknowledgments

The first author was a CONACYT grant holder for the duration of his doctoral studies at CIBNOR (Reg. 60997). The Universidad de Colima and PROMEP also supported our research effort. The research project was supported by a CONACYT grant (990107004). We are grateful to the ATÚN project (CICIMAR-IPN) for providing the capture data. The third author is a SNI grant holder and wishes to acknowledge the support of the Oceanology Division of CICESE and of CICESE's campus at Baja California Sur. We are grateful for the critical analysis and suggestions from two anonymous reviewers and the scientific editor.

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Estimating the encounter rate of Atlantic capelin (*Mallotus villosus*) with fish eggs, based on stomach content analysis

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Abstract—The number of pelagic fish eggs (cod and cunner) found in stomachs of capelin (*Mallotus villosus*) sampled in coastal Newfoundland was used to estimate the encounter rates between capelin and prey, and thus the effective volume swept by capelin. Fish eggs were found in 4–8% of capelin stomachs, represented an average of 1% of prey by numbers, and their abundance increased as relative stomach fullness decreased. The average number of eggs per stomach doubled for each 5-cm increase in length of capelin. The effective volume swept for eggs by capelin ranged from 0.04 to 0.84 m^3/h—a rate that implies either very slow capelin swimming speeds (<1 cm/s) or that fish eggs are not strongly selected as prey. The predation rate estimated from stomach contents was higher than that predicted from laboratory studies of feeding pelagic fish and lower than that predicted by a simple foraging model. It remains uncertain whether capelin play an important regulatory role in the dynamics of early life stages of other fish.

Manuscript submitted 2 November 2004 to the Scientific Editor's Office.
Manuscript approved for publication 10 August 2005 by the Scientific Editor.
Fish. Bull. 104:204–214 (2006).

Capelin (*Mallotus villosus* (Muller, 1776)) is a key species in Arctic ecosystems, serving as a major prey for top predators, from fish to birds and whales (Akenhead et al., 1982; Gjøsæter, 1998; Vilhjálmsson, 2002). Off the coast of Newfoundland and Labrador (eastern Canada), capelin are also the dominant consumers of secondary production (O'Driscoll et al., 2001), as they are in other ecosystems (Skjoldal and Rey, 1989; Hassel et al., 1991). They feed on a wide variety of zooplankton taxa, copepods and euphausiids being the dominant prey (Vésin et al., 1981; Panasenko[1]; Huse and Toresen, 1996; Assthorsson and Gislason, 1997; O'Driscoll et al., 2001). The choice of prey shows some degree of size-dependency; copepod size increases with increasing size of capelin, and euphausiids become more frequent prey items as fish size increases. In most studies of the feeding habits of capelin, fish eggs and larvae have been found to have been eaten by capelin, although these prey types generally represent a minor portion of the diet, occurring in less than 5% of stomachs (Huse and Toresen, 1996; O'Driscoll et al., 2001). Because capelin are dominant consumers of zooplankton in many of the ecosystems in which they are present, their overall impact on the survival of pelagic fish eggs and larvae may be significant depending on their encounter rates with these fish eggs and larvae.

There is evidence that capelin can have a significant impact on the survival of ichthyoplankton through predation on pelagic fish eggs and larvae. In a series of patch studies, Pepin et al. (2002) found that the mortality rate of radiated shanny (*Ulvaria subbifurcata*, Storer 1839) larvae increased in direct relation to hydroacoustic estimates of capelin abundance; this loss could be attributed to predation by capelin on fish larvae. In a study of two coastal areas, differences in the regional patterns of selective loss of radiated shanny larvae, derived from sequential observations of the distribution of growth rates, were strongly associated with differences in the spatial distribution and abundance of capelin (Baumann et al., 2003; Pepin et al., 2003). However, the overall impact of capelin on fish eggs and larvae has been difficult to estimate (Paradis and Pepin, 2001). Much of the basic foraging ecology is unknown (e.g., predator's reactive distance, behavior of both predator and prey, and selection of prey) and laboratory experiments can only provide a rough approximation of encounter rates between capelin and their prey (Paradis et al., 1996).

There have been few studies to provide an estimate of the contribution of predation by planktivorous fish on the overall mortality rates of fish eggs or larvae (Hunter and Kimbrell, 1980; Cowan et al., 1999; Köster and Möllmann, 2000; Munk, 2002; Pepin et al., 2002). Population studies have shown that planktivorous fish can play an important role in regulating the stock-recruitment relationship of other species (Swain and Sinclair,

[1] Panasenko, L. D. 1984. Feeding of Barents Sea capelin. ICES CM 1984/H:6, 16 p.

Table 1

Location, average zooplankton density (all organisms), average fish egg density, and number of capelin (*Mallotus villosus*) stomachs collected at each sampling site.

Site	Latitude	Longitude	Average zooplankton density (/m³)	Average fish egg density (/m³)	No. of stomachs collected at each site					
					00:01–04:00	04:01–08:00	08:01–12:00	12:01–16:00	16:01–20:00	20:01–24:00
1	47°44'N	53°40'W	1255	0.094	50	45	—	—	—	—
2	48°18'N	53°16'W	319	0.91	35	50	17	30	18	48
3	47°44'N	53°38'W	2766	0.23	—	100	22	—	—	—
4	48°02'N	53°36'W	210	0.29	99	50	99	50	9	49
5	48°19'N	53°15'W	3096	0.58	51	49	44	49	49	47

2000; Köster et al., 2001; Garrison et al., 2002). Individual-based models have often served as a tool to infer the potential effect of predators on early life stages (Cowan et al., 1999; Paradis et al., 1999; Werner et al., 2001) where the likelihood of a prey being eaten by a predator is the product of the probabilities of encounter, attack, and capture. Although the latter two components of the predation process have been estimated in the laboratory for a number of species (see Paradis et al., 1996, for a review), encounter rates are often modeled as the product of predator's swimming speed and reactive distance with limited substantive data to support the overall estimate. Furthermore, encounter rates are assumed to occur randomly and thus follow a Poisson distribution; yet there have been few attempts to validate this assumption (but see Huse and Toresen, 2000). Given that encounter rates represent a key parameter required to estimate the potential impact of predators on early life stages, it is surprising that knowledge of this element in the field is so limited.

The goal of the present study was to estimate effective encounter rates of adult capelin with fish eggs and larvae in coastal Newfoundland. The approach was to obtain a high number of specimens from a series of intensive diurnal collections to provide an accurate estimate of the probability distribution of prey numbers from which encounter rates could be derived. The primary focus of this analysis was on the presence and frequency of occurrence of fish eggs as prey for capelin, because they persist longer in stomachs than do fish larvae (Hunter and Kimbrell, 1980; Folkvord, 1993). I used estimates of prey availability from plankton samples combined with the frequency of occurrence of eggs in stomachs, in relation to the size of capelin and time of day, to estimate effective encounter rates (volume searched) by capelin. Fish eggs are well suited to this objective: they are completely passive and thus the probabilities of their avoidance of both plankton nets and predators can be considered as nil. It is thus possible to measure accurately their abundance in the field, given appropriate choice of mesh size, and their numbers in predator stomachs can provide a measure of the effective volume searched, which is the product of the probabilities of encounter and attack.

Materials and methods

The study was conducted in Trinity Bay, Newfoundland, Canada, between 17 and 31 July 2000, as part of a larger program dealing with the dynamics of ichthyoplankton (Baumann et al., 2003). Five sites were selected at which to conduct diurnal sampling of capelin based on the observation of high juvenile and adult capelin densities from hydroacoustic returns. Sampling was conducted within a 3-km radius of each site and at 4-hour intervals over a single twenty-four hour interval. Each site was treated as an independent observation of the diurnal feeding patterns of capelin. As a result of poor catches, sampling was stopped after two sampling periods at the two sites located at the head of the bay (Table 1).

Capelin were sampled using an international young gadoids pelagic trawl (IYGPT) mid-water-trawl towed in a single oblique haul from the surface to a 100-m depth. Each tow lasted approximately 30 minutes. Up to 50 juvenile and adult capelin were taken at random from the catch. When capelin were highly numerous, sample size was increased to 100. For each specimen, total length (TL) was measured to the nearest mm, the entire intestinal tract was removed by cutting the oesophagus as close to the mouth as possible, and the tract was then preserved in individual numbered vials containing 5% formaldehyde. A total of 1052 specimens were obtained from these collections. After each trawl haul, a plankton sample was taken by using a 60-cm bongo net (fitted with 333-µm mesh net and flowmeters) towed obliquely from the surface to 100 m along the same path as the mid-water-trawl, and the sample was preserved in 2% formaldehyde solution.

Stomachs were processed by slitting them open and scraping out the contents onto preweighed aluminium weight boat. The contents were blotted dry to remove all excess liquid and weighed to the nearest 0.01 mg by using a Cahn microbalance. Stomach contents from each capelin specimen were placed into individual petri dishes and examined for the presence, number, and taxonomic identification of pelagic fish eggs only. An egg was counted only when the specimen was complete and

the chorion was relatively intact. The presence of empty chorions was noted but these were not included in the analysis because of their potentially longer residence time in the stomach of predators (Hunter and Kimbrell, 1980). As it turned out, empty chorions occurred in less than 2% of capelin with fish eggs present in their gut. For every fifth capelin specimen, all prey items were identified according to broad taxonomic groups: Copepoda, Amphipoda, Euphausia, Pteropoda, molluscan veligers, brachyuran zoeae, Larvaecea, Cladocera, Chaetognatha, Isopoda, and fish eggs and larvae. The number of individuals was determined for each taxonomic group from the entire stomach content and the total weight for each group was determined to the nearest μg by using a Cahn microbalance. This protocol was followed to provide a complete assessment of the presence of fish eggs in the gut and to provide a representative assessment of the patterns of prey composition from each site to confirm that general feeding patterns were consistent with results from previous studies. O'Driscoll et al. (2001) had performed a detailed analysis of feeding patterns of capelin in Newfoundland waters and I perceived no need or advantage in repeating the work. The complete analysis of stomach contents was performed on 218 capelin specimens.

All fish eggs and larvae were sorted from plankton samples and identified to the lowest taxonomic level possible. Because of difficulties in differentiating early developmental stages of two species groups, eggs were lumped into either of two groups: 1) CHW (namely, cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and witch flounder (*Glyptocephalus cynoglossus* L.) or 2) CYT (cunner (*Tautogolabrus adspersus* L.), yellowtail flounder (*Limanda ferruginea*, Storer 1839)). Eggs were most likely those of cod, for the CHW category, and cunner, for the CYT category because only larvae of those species were found in other elements of the research program. A subsample of other zooplankton, yielding 200–300 specimens, was identified to the lowest taxonimic level possible.

For each capelin, the total gut fullness index (GFI) was estimated as $GFI=W_s/W$, where W_s=the weight of stomach contents (g); and W=is the weight of the fish (g), based on the local bias-corrected length-weight relationship ($\log_{10} W=-6.44+3.38 \log_{10} TL$, where W=weight in g and T=total length in mm; $r^2=0.98$; and the standard error of the intercept and slope are 0.049 and 0.023; Mowbray[2]).

Analysis

Stomach content composition

For each capelin on which the full stomach contents were analyzed, the number of each major prey taxon was determined. These data, arcsine-square-root transformed, were contrasted using principal component analysis in which the proportion of prey type, log-transformed capelin length and GFI were included to determine if the observations from this study were consistent with those from previous ones.

Frequency of fish eggs

The probability distribution of egg numbers per gut was contrasted with the expectations based on a Poisson process. Encounters between predator and prey can be described by using a modification of Gerritsen and Strickler's (1977) equations where

$$\lambda = \pi \cdot R^2 \cdot A_{prey} \cdot \sqrt{u^2 + v^2}, \quad (1)$$

where R = the reactive distance (m);
A_{prey} = the density of prey (/m^3); and
u and v = the swimming speeds of predator and prey (m/h), which yields an encounter rate λ (per h).

Huse and Toresen (2000) used laboratory estimates of the various parameters to estimate encounter rates between juvenile herring (*Clupea harengus* L.) and capelin larvae. Instead of using their approach, I chose to reduce Equation 1 to its simplest form, such that

$$\lambda = K \cdot A_{prey}, \quad (2)$$

where K = the effective volume swept (m^3/h) during the period during which eggs will remain discernible in the gut of capelin; and
A_{prey} = the observed density of eggs (/m^3) in the water column from plankton samples.

The resulting probability of finding N prey in the gut of capelin then becomes

$$P(N) = \frac{\lambda^N}{N!} \cdot e^{-\lambda}, \quad (3)$$

where λ = the mean encounter rate.

Mean number of eggs per stomach (N), taken as a measure of encounter rates for each four-hour sampling interval, was estimated by fitting a generalized linear model with Poisson error structure using a log link function by maximum likelihood (GENMOD procedure, vers. 8, SAS Inc., Cary, NC) to the data from all 4-hour sampling intervals (T) from all locations, with TL of individual capelin as a linear covariate.

$$f(N) = b_0 + b_1 T + b_2 TL. \quad (4)$$

The value of N reported in the "Results" section is the least squares adjusted mean, which represents the value of the average length of capelin from field collections. We attempted to include site into the analysis but the

[2] Mowbray, F. 2005. Personal commun. Fisheries and Oceans, St. John's, Newfoundland, Canada.

algorithm failed to converge because of missing observations. Effective volume swept (K) was calculated from the estimated mean number of eggs per stomach (as a measure of encounter rates) and the estimated density of eggs based on plankton samples by re-arranging Equation 2 and assuming that encounters between prey and predators were random over the top 100 m of the water column. I define K as the effective volume swept because it implicitly includes some measure of the probabilities of attack and capture. Values of the estimated volume swept were corrected for evacuation rates. Hunter and Kimbrell (1980) found that the evacuation rate of northern anchovy (*Engraulis mordax*, Girard 1854) feeding on fish eggs at 15°C was ~50%/h based on an exponential model (exponential rate of 0.7/h), which is appropriate for microphagic fish (Temming et al., 2002). Based on the duration of our tow and the handling time to process the samples, the observations of stomach content from this study represent 50% of the eggs consumed during the last hour before capture. Hunter and Kimbrell's (1980) estimate of the evacuation rate is approximately twice that obtained in field studies by Arrhenius and Hansson (1994) and Darbyson et al. (2003) for herring (*C. harengus* L.) feeding primarily on copepods. However, the estimates from the latter two studies were based on total gut fullness and not on the disappearance of specific food items, such as fish eggs. As a result, Hunter and Kimbrell (1980) provided the only current measure of the rate of disappearance of eggs in the stomachs of planktivorous fish. Increases or decreases in evacuation rates because of inaccuracies in our knowledge of the rate of disappearance of eggs from stomach contents will result in corresponding changes in the estimate of the effective volume swept. By using the mean number of eggs per stomach as an estimator of the effective volume swept, the probabilities of attack and capture within the reactive distance are assumed to be 100%. The resulting value of the effective volume swept represents an average over the top 100 m of the water column, the depth range over which we sampled both capelin and zooplankton and over which I assume that the encounters are random. Ideally, one would want to obtain a depth-stratified measure of stomach contents, and prey availability and overlap between prey and predator, such as has been inferred in the Baltic Sea (Köster and Möllmann 2000; Köster et al. 2001), but this was not possible in the present study because there were insufficient data on the vertical distribution of capelin.

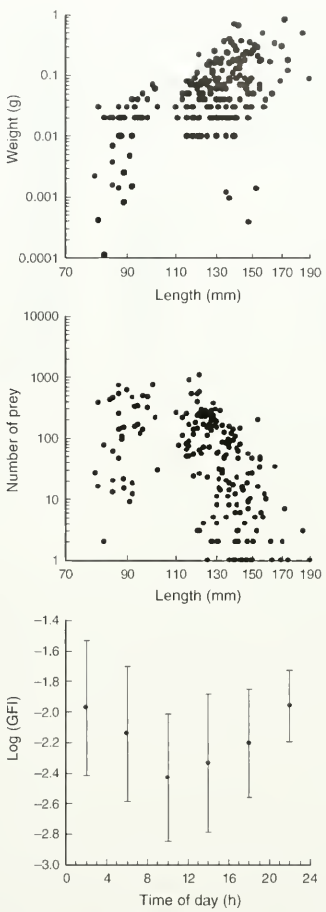

Figure 1

Weight of stomach contents (upper graph) and number of prey per stomach (center graph) in relation to capelin (*Mallotus villosus*) length, for specimens with complete analysis of contents, and average and standard deviation of the log-transformed gut fullness index (GFI) in relation to time of day (lower graph), based on all fish sampled. Statistics were calculated for all samples collected within each 4-hour time interval.

Results

Capelin used in this analysis ranged from 53 to 195 mm TL (mean=122 mm; median=130 mm). Average zooplankton concentrations ranged from 210 to 3096 organisms/m^3. In most samples, the copepods *Calanus finmarchicus* and *Pseudocalanus* sp. and the larvacean *Fritillaria borealis* (Lohmann 1896) represented 60–80% of the zooplankton by number, based on samples from bongo nets. In both species of copepods, copepodite stages II and III were most abundant. A finer mesh net would have revealed that *Oithoina similis* was also

Table 2

Frequency of occurrence (number of capelin [*Mallotus villosus*] for which complete stomach analysis was performed) and average relative proportion of prey (by number) for the dominant prey categories found in July 2000. The total number of capelin examined for complete stomach analysis was 218. There were 12 fish with empty stomachs.

Prey type	Frequency of occurrence	Relative proportion
Copepoda	176	0.77
Euphausia	50	0.066
Amphipoda	43	0.088
Pteropoda	22	0.010
Larvacea	21	0.032
Cladocera	17	0.022
Fish eggs	16	0.010
Chaetognatha	4	<0.001
Mollusca veliger	3	0.001
Brachyura zoea	2	0.005
Isopoda	1	<0.001

Table 3

Results of the principle components (PC) analysis of proportion of prey categories from capelin stomachs. Values in parentheses along the topmost row represent the proportion of the variance explained by each principle component. Column values represent the average loading of each variable included in the analysis. *GFI*= gut fullness index.

Variables	PC 1 (17%)	PC 2 (12%)	PC 3 (10%)
Ln (*capelin length*)	0.494	−0.068	−0.144
Ln (*GFI*)	0.166	−0.575	0.325
Copepod	−0.598	−0.276	−0.081
Cladocera	−0.035	0.315	0.593
Pteropoda	0.044	−0.131	−0.050
Amphipoda	0.490	−0.017	−0.026
Euphausia	0.330	−0.153	0.122
Cheatognatha	−0.066	−0.083	−0.110
Mollusca	−0.017	0.260	0.550
Isopoda	−0.023	0.003	−0.173
Larvacea	−0.011	0.440	−0.065
Brachyura	0.038	0.280	−0.310
Fish eggs	0.106	0.340	−0.232

numerically important in the area (Pepin and Maillet[3]), but O'Driscoll et al. (2001) did not find this species in any of their stomach samples despite its importance in the regional plankton community. Fish eggs represented an average of 0.13% of the total zooplankton community among all sites sampled (Table 1).

Only 12 of 218 capelin stomachs, for which complete stomach analysis was performed, were found to be empty. The weight of prey in capelin stomachs increased with increasing length but the number of prey decreased with increasing length, indicating that the average size of prey increased with capelin length (Fig. 1). Stomach fullness increased at sunset, peaked shortly after midnight, and then gradually decreased during the remainder of the night and day (Fig. 1). Copepods were the only prey in 73 of the remaining 206 capelin. Euphausiids and amphipods were the next most abundant prey item, found in approximately 25% of capelin stomachs and representing on average 6.5% and 8.8% of prey by number (Table 2). Pteropods, larvaceans, cladocerans and fish eggs were present in approximately 10% of capelin stomachs and represented ~1–3% of prey by numbers (Table 2). Other prey taxa were found in a few capelin stomachs. Principal components analysis showed that the proportion of euphausiids and amphipods in stomachs increased with capelin length, whereas copepods were more frequent in smaller fish, as indicated by the first principal component (Table 3). Other prey categories, particularly fish eggs and larvaceans, were generally more likely to occur in capelin stomachs when they were relatively empty, as indicated by the second principle component (Table 3). Finally, the third principal component indicated that fish eggs appeared to be less important in areas where mollusks and Cladocera were more frequent in the diet of capelin—a finding that possibly reflects the influence of water masses in which coastal rather than shelf zooplankton were dominant (Table 3). These observations of prey composition were generally consistent with those of O'Driscoll et al. (2001).

When we consider all stomachs analyzed for fish eggs, the overall frequency of occurrence of fish eggs was 4.3% (46 of 1052 stomachs). This is less than the value (7.9% of stomachs with prey) obtained from those stomachs with complete analysis of prey composition. The frequency distribution of fish eggs was well described by a Poisson distribution (Fig. 2). The majority of fish eggs (89%) were of the CHW complex and the remainder (11%) were of the CYT complex. The generalized linear model revealed that there was a significant effect of time of day (Table 4), and the greatest number of fish eggs in capelin stomachs were found between 20:00 and 24:00, following sunset, and the lowest numbers were found between 00:00–04:00 (Fig. 3). There was approximately a 20-fold difference in the least squares

[3] Pepin, P., and G. L. Maillet. 2002. Biological and chemical oceanographic conditions on the Newfoundland Shelf during 2001 with comparisons with earlier observations. Canadian Science Advisory Secretariat, Research Document 2001/073, 60 p. [Available from http://www.dfo-mpo.gc.ca/csas/ or Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, 200 Kent Street, stn. 12032, Ottawa, Ontario, Canada K1A 0E6.]

Table 4

Analysis of deviance for the effects of time of day and capelin TL with Poisson error based on a generalized linear model. The effect of time of day was based on grouping data into 4-hour classification periods. Probability values were calculated by using a χ^2 function.

		Difference			
Variable	Residual degrees of freedom (df)	Residual deviance	df	Deviance	*P*
	1052	365.9			
Time of day	1046	321.7	6	44.2	<0.001
Length	1045	317.2	1	4.5	<0.05

mean estimate of the number of eggs per stomach over a diurnal cycle. There was a significant and positive effect due to capelin length (χ^2=4.5, P<0.05; Table 4) which would yield a twofold increase in the mean number of eggs per stomachs for each 5-cm increase in capelin length. This finding may indicate that smaller capelin are more effective predators of fish eggs, in terms of body mass, than larger individuals. There were insufficient data to obtain reliable estimates of the diurnal feeding periodicity at each site.

The overall unweighted average density of fish eggs among all sites was 0.52/m^3 (median=0.48/m^3; mean=0.53/m^3; SD=0.43/m^3; range=0.09–2.2/m^3). There were significant differences in the densities of fish eggs among sites (ANOVA $F_{4,21}$=4.56, P<0.01); a Bonferoni *post hoc* comparison revealed that site 2 had significantly higher densities than other sites, with the exception of site 5 (Table 1). However, there was no clear evidence of a diurnal pattern to the density estimates derived from plankton collections. Because there were insufficient data to obtain reliable estimates of the diurnal feeding periodicity at each site and because there was no clear evidence of a diurnal pattern in egg densities estimated from the plankton samples, I chose to use the overall unweighted average density from all collections as the estimate of A_{prey} for Equation 2.

Because it was not possible to obtain a site-specific estimate of diurnal patterns in egg consumption by capelin, the combined data on egg densities were used to estimate the effective volume swept (K). Each estimate of the mean number of eggs per stomach was taken to represent 50% of the eggs ingested in the last hour during each sampling interval (4 h) (see "Methods"). The overall daily average effective volume swept based on mean encounter rates was 0.27 m^3/h, which ranged from 0.04 m^3/h at night (00:00–04:00) to 0.84 m^3/h following sunset (20:00–24:00) (Fig. 4). Based on a reactive distance of 0.15 m (~1 body length) used by Huse and Toresen (2000) (for herring larvae from Utne-Palm, 2000), the effective volume swept estimated from the observations reported in the present study would imply that the swimming speed of capelin would be very low (≤1 cm/s) or that fish eggs are not strongly selected as prey during feeding. If on the other hand we consider modal capelin (0.13 m) swimming at 0.5–1 body length/s, the reactive distance would range from 0.024–0.034 m at the time of peak foraging activity, assuming 100% probability of attack within the reactive area. To determine the effect of variations in the density of eggs encountered by capelin, I also calculated the variability

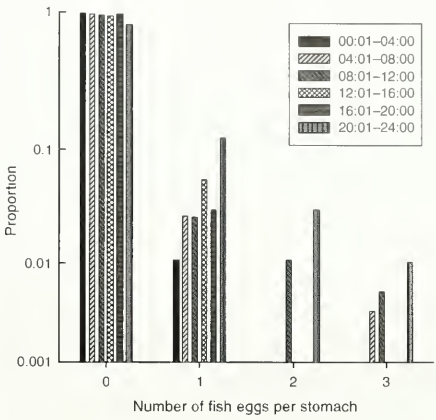

Figure 2

Bar chart of the frequency of fish eggs in capelin (*Mallotus villosus*) stomachs for each 4-hour time interval.

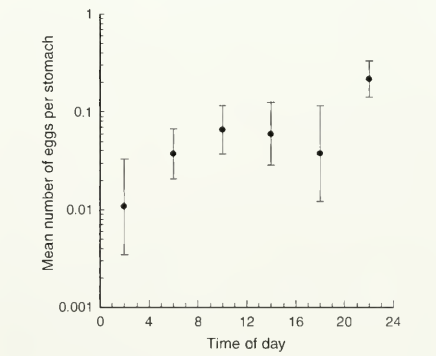

Figure 3

Least squares estimates of the mean number of fish eggs per stomach in relation to time of day. Error bars represent 1 standard error.

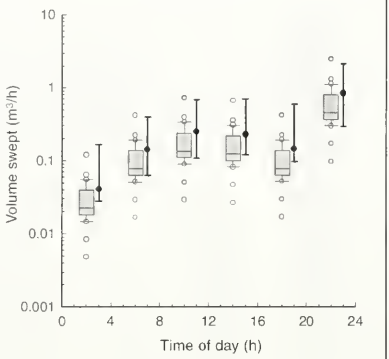

Figure 4

Estimated effective volume swept (K), with ±1 standard error (solid symbols and thick error bars) based on mean number of eggs per stomach and mean density of eggs from plankton collections, in relation to time of day (offset by +1 hour from midpoint of interval). Confidence intervals are based on the maximum likelihood estimates of mean numbers of eggs per capelin stomach. Box plots show the 25th, 50th, and 75th percentiles of the estimated effective volume swept (K) based on the mean number of eggs per stomach and each estimate of egg density based on plankton collections; whiskers show the 10th and 90th percentiles of the distribution and open symbols show the outlying points.

in estimated K using each observation of egg density from the plankton samples. This calculation generally resulted in less variability in the estimate of effective volume swept than the uncertainty in eggs per stomach (Fig. 4, box plots) because of the skewed distribution of egg densities based on plankton tows. The latter reflects the skewed distribution of egg densities based on plankton tows.

Discussion

Capelin prey composition observed in this study is consistent with that observed in previous studies, which show that copepods, euphausiids, and amphipods represent the principal prey items; the overall results of this study may therefore have general applicability. Fish eggs represent a relatively minor part of the diet of capelin. Neither Huse and Toresen (1996) nor Assthorsson and Gislason (1997) reported any occurrence of pelagic fish eggs in the stomachs of capelin from the Barents Sea and waters north of Iceland. O'Driscoll et al. (2001) reported an occurrence of less than 1% in capelin sampled during May–June in inshore waters and during August–September in offshore areas off Newfoundland. In the present study, an occurrence of 4% to 8%, which contributed an average of 1% of prey by numbers, was found for collections in coastal Newfoundland waters during July. There is little basis for explaining the differences between studies because only this analysis provides an estimate of the density of eggs in the water column where capelin were sampled. Fish eggs were approximately 1% of the prey found in the stomachs of capelin but they represented slightly more than 0.1% of the organisms sampled by the plankton nets used in this study. Huse and Toresen (1996) collected plankton data with different gear than that used in the present study, but they did not report the occurrence of pelagic fish eggs in their samples, possibly because pelagic fish eggs were in very low abundance or were absent during the collection periods of their study.

In general, fish eggs were more likely to be found in capelin stomachs as the length of individual fish increased. These fish tend to feed more heavily on larger prey types (e.g., euphausiids and amphipods) but the occurrence of fish eggs in individual fish tended to increase as the relative stomach fullness decreased. When considered with the general pattern in feeding periodicity, fish eggs were more likely to be eaten at the onset of feeding activity shortly after dusk, but as individual fish filled their guts with larger or more numerous prey, feeding on fish eggs tended to decrease. Fish eggs may represent an attractive prey for capelin capable of feeding on larger prey types (e.g., stage V of *C. finmarchicus*, euphausiids, and amphipods) because their weight is comparable to that of large copepods (Darbyson et al., 2003). However, as larger prey types are encountered or as hunger decreases, capelin may become more selective feeders and focus their foraging on energetically more profitable prey. The diurnal pattern of occurrence of fish eggs in capelin stomachs may also reflect differences in the visibility of eggs as a result of changing light levels, as well as predator hunger. Alternatively, the greater number of eggs in stomachs at dusk may reflect increased spatial overlap between predator and prey as capelin move toward the surface in the evening to feed (O'Driscoll et al.[4]).

The effective volume swept by capelin estimated in the present study indicates that the probability that a capelin will attempt to eat a pelagic fish egg is low, because it is highly unlikely that fish will swim at a very slow speed based on an assumed reactive distance. The predation rates based on average densities and encounter rates range from 0.04 to 0.86 egg/h

[4] O'Driscoll R. L., J. T. Anderson, and F. K. Mowbray. 2001b. Abundance and distribution of capelin from an acoustic survey in conjunction with the 1999 pelagic juvenile survey. Capelin in SA2 + Div. 3KL during 1999, Canadian Science Advisory Secretariat Research Document 2001/161. [Available from http://www.dfo-mpo.gc.ca/csas/ or Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, 200 Kent Street, stn. 12032, Ottawa, Ontario, Canada K1A 0E6.]

based on an evacuation rate of 50% of eggs per hour. A low predation rate on fish eggs is not entirely unexpected. The eggs of cunner and cod from our samples had an average diameter of 0.86 and 1.3 mm, whereas the modal length of capelin from our collections was approximately 130 mm, making the eggs ~1% of the predator's body length. Based on Paradis et al.'s (1996) analysis, maximum predation rates by fish feeding on ichthyoplankton occur when the prey are 10% of the predator's length, and the minimum predation rates were observed when prey were ~0.5–1% of the predator's length. Paradis et al.'s (1996) summary equations indicate that an average predation rate of 0.007–0.03 eggs/h would not be inconsistent with laboratory estimates of predation rates for a range of evacuation times from 1 to 4 hours and would be considerably lower than the predation rates estimated in the present study. However, estimates based on a simple foraging model (e.g., Paradis et al., 1999) for a modal capelin swimming at 1 body length/s and with a reactive distance of 1 body length yield a mean of 12 eggs/h, and halving these parameter values yields a predation rate of 1.6 eggs/h. These alternative methods of estimating predation rates indicate that capelin are somewhat more likely to feed on fish eggs in the field than laboratory studies would indicate but less likely than would be anticipated from a simple foraging model. The results from this study do not provide an exhaustive estimate of encounter rates between capelin and pelagic fish eggs, but the range of effective encounter rates derived from the different approaches highlights the lack of understanding of this key parameter essential for any model of multispecies interactions. Such a broad range of expected predation (and encounter) rates indicates that in order to develop predictive skills in estimating the potential impact of planktivores on fish eggs, a better understanding of the factors that prompt a predator to feed on a fish egg is needed. Most laboratory studies dealing with predation by fish on fish eggs and larvae have used single prey and few have provided a measure of the probability of attack (Bailey and Houde, 1989; Paradis et al., 1996). Feeding patterns can be affected by the complexity of the available prey community (Kean-Howie et al., 1988; Gotceitas and Brown, 1993; Pepin and Shears, 1995), but methods to relate prey consumption with prey availability in the field are still limited.

Uncertainty in encounter and predation rates are due partly to errors in the estimation of prey availability and stomach content and partly due to our general lack of knowledge concerning the evacuation rate of fish eggs from predator stomachs. For this study I relied on Hunter and Kimbrell's (1980) observations of evacuation rates for northern anchovy from experiments conducted at 15°C. Water temperatures in Trinity Bay in July 2000 showed considerable variation with depth, ranging from ~13°C at the surface to ~1°C at 100 m, with the overall average temperature over the water column being ~3–4°C. Given that most metabolic processes increase by 1.3–2 times over ten degrees Celsius (e.g., Brett and Groves, 1979), evacuation rates in the present study could have been half of those measured by Hunter and Kimbrell (1980) and thus would imply that our observations of stomach contents could represent 70% of the eggs consumed in the last hour rather than the 50% assumed in the analysis. The result would be that estimates of volumes swept by capelin would have to be reduced by ~30%, further reducing their potential impact on ichthyoplankton populations. The general uncertainty in our knowledge of evacuation rates for fish eggs from the stomachs of capelin, and from most other planktivorous fish, therefore limits the inferences that can be derived about their impact on ichthyoplankton survival.

A second source of uncertainty is due to the inherent sampling variability associated with the study of elements that form a small fraction of the prey of a predator. This study was based on more than 1000 specimens from a small region in order to provide the greatest accuracy possible within the confines of the study area. Stomach sampling is often restricted to fewer specimens sampled over a much broader geographic range. Without a large number of observations from a local environmental setting (i.e., site), estimates of mean numbers of rare prey types would likely be unable to reflect the effect of site-specific differences in environmental conditions on predator feeding and would thereby increase the uncertainty around the estimated effective encounter rates. The situation is well illustrated by the doubling in the frequency of occurrence of fish eggs in the specimens that were randomly selected for complete gut analysis versus all the specimens collected for analysis. Further uncertainty comes from the variability in estimates of egg density encountered by capelin—a variability that tended to result in slightly tighter confidence intervals in estimates of effective volume swept than the uncertainty due to variability in the number of prey per predator stomach. Variations in egg densities from plankton samples did result in lower estimates of effective volume swept, partly as a result of the rare high densities (typical of highly skewed distribution) that characterize the variability in plankton catches (Power and Moser, 1999). Although this study is not intended to provide a general estimate of the effective encounter rate of capelin feeding on fish eggs, the approach provides a useful example of the sampling requirements for the study of feeding on prey that are a minor part of the diet of a predator but which may be greatly affected by the predator's impact on the prey population.

Greater efforts must be directed at understanding patterns of predation in the field, in relation to prey availability, if the role of planktivorous fish in ichthyoplankton dynamics is to be understood. The assumptions in the estimation approach could affect the effective volume swept: estimates of the effective volume swept are based on average prey densities integrated over the water column, and the simplification of the encounter model (Eq. 1) incorporates possible variations in the probability of attack (e.g., due to diurnal variations in visibility of eggs) into the value of K. Pepin et

al. (2005) noted that in the study region, pelagic fish eggs are generally more abundant near the surface and decrease exponentially in abundance with increasing depth. As a result, if feeding by capelin occurs predominantly in surface waters, the effective density of prey encountered would be greater than the average density over the water column, which would in turn decrease the estimate of the effective volume swept based on our estimates of encounter rates. However, the patterns of vertical distribution of both eggs (Pepin et al., 2005) and capelin (O'Driscoll et al., 2001) are highly variable among sites and without accurate estimates of these elements from the current study, inferences about the impact on estimates of the effective volume swept would be speculative. In contrast, I implicitly incorporated the probability of attack into the estimate of the effective volume search, essentially giving it a value of 100%. However, Wieland and Köster (1996) found that the visibility of eggs increased with developmental stage and hence may alter the probability of attack by a predator. Lower visibility of early stage eggs could lead to an increase in the estimate of the effective volume swept, but because we could not stage most eggs sampled from the stomachs, the net effect on the estimated volume swept is unclear.

Planktivorous fish represent important forage for piscivores in several marine ecosystems but they can also play a significant role as predators of early life stages. In the Baltic Sea, spratt (*Sprattus sprattus* L.) feed extensively on cod eggs (Köster and Möllmann, 2000) and they may play an important role in regulating the underlying form of the stock-recruitment relationship (Köster et al., 2001). In upwelling systems, anchovies and sardines may also have a significant impact on egg and larval mortality rates (Smith et al., 1989). It has also been suggested that herring (*C. harengus* L.) and mackerel (*Scomber scombrus* L.) predation on ichtyplankton may play an important role in fish population dynamics in the Gulf of St. Lawrence (Swain and Sinclair, 2000) and on Georges Bank (Garrison et al., 2002). However it is unclear whether capelin play a significant role in the fish community dynamics in the ecosystems they inhabit, despite evidence that they are likely to have a significant impact on zooplankton abundance (Vésin et al., 1981; Akenhead et al., 1982; Skjoldal and Rey, 1989; Hassel et al., 1991). Clupeids, scombrids and engraulids can alternate between filter- and particulate-feeding modes, which may allow them to more effectively consume relatively small prey (~1 mm), such as fish eggs. There is no information on the feeding modes of capelin, but another osmerid, rainbow smelt (*Osmerus mordax*, Mitchill 1814), is known to be a primarily particulate feeder (Mills et al., 1995). Particulate feeding is generally directed toward larger prey, whereas filter feeding is used when prey are smaller or more abundant. Gill raker structure does not provide significant insight into the possible feeding modes of these various planktivorous fish. The estimate of reactive distance from the present study (0.024–0.034 m) is of the same order as the gape width of capelin (3.6% for TL; Pepin, unpubl. data), making filter feeding a distinctly possible mode of feeding. For known filter feeders, Uotani (1985) reported a maximum gill raker length of 6 mm in *Engraulis japonicus* (100 mm TL), Gibson (1988) reported an average gill raker length of 4 mm in *Clupea harengus* (150 mm TL), and Molina et al. (1996) reported gill raker lengths ranging from 5 to 9 mm in *Scomber japonicus* (150–250 mm SL). On the other hand, Lecomte and Dodson (2004) reported gill raker lengths of 3.3–3.9 mm in *Osmerus mordax* (150 mm TL). In the case of capelin, I found that gill rakers ranged from 3.0–4.5 mm in length (130–170 mm TL) (Pepin, unpubl. data). Inter-raker gaps among all these species ranges from 0.19 mm (*E. japonicus*) to 0.4 mm (*S. japonicus*) and from 0.36 to 0.45 mm in capelin (Pepin, unpubl. data). Thus all these species, which feed extensively on zooplankton but which use different ingestion modes, are equipped with gill rakers designed to retain small particles. To better understand the role of capelin in Arctic ecosystems, a greater knowledge of feeding will be required. If filter feeding is a dominant feeding mode, a simple filtration or volume-swept model may provide an accurate measure of the potential impact of capelin on fish eggs, whereas greater knowledge of behavior and selectivity will be required if particulate feeding is the dominant feeding mode because selection for or against fish eggs could be influenced by availability of alternate prey (e.g., Kean-Howie et al., 1988).

In most of the areas where planktivores can have a significant impact on the mortality of fish eggs, the ecosystems can be characterized as being "wasp-waisted" (Cury et al., 2000), i.e, as having a relatively high diversity of plankton species and top predators that are all influenced by the abundance and productivity of relatively few and dominant forage fish species that act to transfer energy from secondary producers to upper trophic levels in a manner similar to that found in many Arctic regions. It is clear that capelin are important prey for a number of top predators in the waters of the Barents Sea (Gjøsæter, 1998), Iceland (Vilhjálmsson, 2002), and on the Newfoundland and Labrador coast (Akenhead et al., 1982), and they may also have an important impact on the plankton community (Skjoldal and Rey, 1989; Hassel et al., 1991). What remains uncertain is whether they play an important regulatory role in the dynamics of the early life stages of fish. Observations from this study revealed that the highest occurrence of fish eggs in the stomachs of capelin came from capelin near one of the few remaining major spawning aggregations of the northern cod stock (Rose, 2003). The dynamics of such circular prey-predator interactions need to be studied further in order to understand their potential importance to population regulation (Walters and Kitchell, 2001) but to do so will require consideration of the spatial and temporal patterns of predator-prey interactions if predictive relationships are to be derived (Pepin et al., 2002, 2003; Baumann et al., 2003).

Acknowledgments

I would like to thank Tim Shears, Gary Maillet, Hugh Maclean, and Greg Redmond for their assistance in the field, Leah Wilson for performing the laboratory analysis of stomach contents, and the officers and crew of the *CCGS Templeman* for their diligence. Comments by J. Carscadden, J. Dower, G. Huse, F. Mowbray, and two anonymous referees helped to improve the manuscript.

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A production modeling approach to the assessment of the horseshoe crab (*Limulus polyphemus*) population in Delaware Bay

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Abstract—Horseshoe crab (*Limulus polyphemus*) is harvested commercially, used by the biomedical industry, and provides food for migrating shorebirds, particularly in Delaware Bay. Recently, decreasing crab population trends in this region have raised concerns that the stock may be insufficient to fulfill the needs of these diverse user groups. To assess the Delaware Bay horseshoe crab population, we used surplus production models (programmed in ASPIC), which incorporated data from fishery-independent surveys, fishery-dependent catch-per-unit-of-effort data, and regional harvest. Results showed a depleted population (B_{2003}/B_{MSY}=0.03–0.71) and high relative fishing mortality (F_{2002}/F_{MSY}=0.9–9.5). Future harvest strategies for a 15-year period were evaluated by using population projections with ASPICP software. Under 2003 harvest levels (1356 t), population recovery to B_{MSY} would take at least four years, and four of the seven models predicted that the population would not reach B_{MSY} within the 15-year period. Production models for horseshoe crab assessment provided management benchmarks for a species with limited data and no prior stock assessment.

Manuscript submitted 25 January 2005 to the Scientific Editor's Office.

Manuscript approved for publication 10 August 2005 by the Scientific Editor.

Fish. Bull. 104:215–225 (2006).

The horseshoe crab (*Limulus polyphemus*) has become a source of controversy on the Atlantic coast of the United States (Berkson and Shuster, 1999; Walls et al., 2002). This species is commercially harvested for use as bait, is used by the biomedical industry, and is an important source of food for a large number of species, including migrating shorebirds. However, population trends in the Delaware Bay region in recent years have indicated a possible decline in horseshoe crab abundance, raising concerns that the population may be unable to fulfill the present and future needs of these diverse user groups.

Horseshoe crabs are harvested commercially for use as bait in the American eel (*Anguilla rostrata*), whelk, and conch (family Melongenidae) pot fisheries (ASMFC[1]). Historically, horseshoe crabs were considered "trash fish" of little commercial value and were used primarily as fertilizer or animal feed. When the bait fishery began, there were few restrictions on harvest and no harvest-reporting requirements. A maximum reported coastwide harvest of about 2 million crabs (3100 metric tons [t]) occurred in 1998 (ASMFC[2]). Commercial harvest has decreased in recent years owing to the adoption of state-by-state quotas in 2000 (ASMFC[3]) and the increased use of bait-saving devices for the eel and conch fisheries, both of which have reduced the demand for crabs.

Horseshoe crabs are also used by the biomedical industry. The blood of horseshoe crabs contains *Limulus* Amebocyte Lysate (LAL), a substance used to detect the presence of endotoxin contamination in injectable and implantable drugs and devices (Novitsky, 1984). The Food and Drug Administration estimated that 260,000 horseshoe crabs were bled for LAL in 1997. After bleeding, the animals were released at the capture site, and

[1] ASMFC (Atlantic States Marine Fisheries Commission). 1998. Interstate fishery management plan for horseshoe crab, 57 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[2] ASMFC. 2004. Horseshoe crab 2004 stock assessment report, 87 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[3] ASMFC. 2000. Addendum I to the fishery management plan for horseshoe crab, 9 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

the mortality from the bleeding process was estimated to be 7.5% (Walls and Berkson, 2003). Currently, there is no substitute for LAL that offers comparable speed and sensitivity.

Horseshoe crabs also play an important role in marine and terrestrial food webs (Botton and Shuster, 2003). Shorebirds migrating from South America to Arctic breeding grounds stop in the Delaware Bay to rebuild depleted energy reserves (Botton et al., 1994). The time and place of their stop-over coincides with that of annual horseshoe crab breeding, when the crabs arrive en masse to spawn on sandy beaches during high tides of May and June (Botton and Harrington, 2003). An adult female horseshoe crab lays approximately 88,000 eggs per year (Shuster, 1982), and a single red knot (*Calidris canutus*) can consume an estimated 18,000 crab eggs daily (USFWS[4]).

Horseshoe crabs account for substantial economic value in the Delaware Bay region. Regional economic contribution of the eel and conch fisheries is approximately $2.2 to $2.8 million annually. The regional economic value of the horseshoe crab biomedical industry is $26.7 to $34.9 million annually. Ecotourism related to migrating shorebirds has become increasingly important to the economy of the Delaware Bay region. An estimated 6,000 to 10,000 recreational bird watchers visit the Delaware Bay in spring and contribute $6.8 to $10.3 million to the regional economy.

Recently, there has been concern that the horseshoe crab population can fulfill the current needs of these user groups. These concerns led the Atlantic States Marine Fisheries Commission (ASMFC) to develop a fishery management plan for horseshoe crabs. Unfortunately, very few abundance data are available for this species. Many state and federal trawl surveys record horseshoe crabs caught during sampling, but gear and sampling methods are not designed for horseshoe crabs and catches are not common. Only recently have statistically robust horseshoe crab-specific surveys been initiated: a Delaware Bay spawning survey (Smith et al., 2002) and an offshore trawl survey (Hata and Berkson, 2003).

Because of the limited data available, previous stock assessments of the Delaware Bay population have been restricted to trend analyses to determine whether a single survey identifies a significant change in the population or whether there is a consensus among data sets. However, many Delaware Bay surveys have high variability and low power to detect population change and would therefore only be able to identify dramatic changes in population size. Also, trend analyses do not provide estimates of stock status (Caddy, 1998) such as relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}). The ultimate goal for horseshoe crab assessment employs a stage-based catch-survey methodology (Collie and Sissenwine, 1983; HSC-SAS[5]), incorporating data from harvest and surveys. It will be a number of years before this modeling approach can be implemented, however, since stage-class data from commercial harvest are not currently being collected.

The surplus production modeling approach (Prager, 1994) used in our study is an appropriate bridge between these two methods. Production models allow for the incorporation of harvest data and multiple surveys, improving predictive power over that of a single survey. This technique does not include a stage-structure in the model; instead it focuses on the dynamics of the population as a whole. Similar methods have been successfully applied to horseshoe crab data from Rhode Island (Gibson and Olszewski[6]) and production models have been widely used for assessments of other species (Booth and Punt, 1998; Cadrin and Hatfield, 2002; Vaughan and Prager, 2002). Surplus production models assume a low population growth rate at small population sizes and as the population nears the carrying capacity (Quinn and Deriso, 1999). In the logistic growth form of the model used in the present study, maximum growth rate (and maximum surplus production) occurs at one-half of the carrying capacity. At this point, the maximum surplus population growth can be harvested while still maintaining a stable population size. Surplus production models provide estimates of maximum sustainable yield (MSY; the largest harvest that can continuously be removed from a stock), population biomass, and fishing mortality, as well as allow for the estimation of effects of future management.

We fitted a regional-scale production model to Delaware Bay horseshoe crab data in order to quantify the current status of the Delaware Bay population and to estimate impacts of future management actions. The results from this production model will allow the ASMFC and member states to manage the Delaware Bay population of horseshoe crabs more effectively with the goal of providing a sustainable resource for commercial harvest, the biomedical industry, and migrating shorebirds.

Methods

Production model

We used an age-aggregated production model with the Prager (1994) form of the Graham-Schaefer surplus-production model (i.e., logistic population growth),

[4] USFWS (U.S. Fish and Wildlife Service). 2003. Delaware Bay shorebird-horseshoe crab assessment report and peer review. Migratory Bird Publication R9-03/02, 107 p. USFWS, 4401 N. Fairfax Dr., MBSP 4107, Arlington, VA 22203.

[5] HSC-SAS (Horseshoe crab stock assessment subcommittee). 2000. A conceptual framework for the assessment of horseshoe crab stocks in the mid-Atlantic region, 19 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[6] Gibson, M., and S. Olszewski. 2001. Stock status of horseshoe crabs in Rhode Island in 2000 with recommendations for management, 13 p. RI Division of Fish and Wildlife, 4808 Tower Hill Rd., Wakefield, RI 02879.

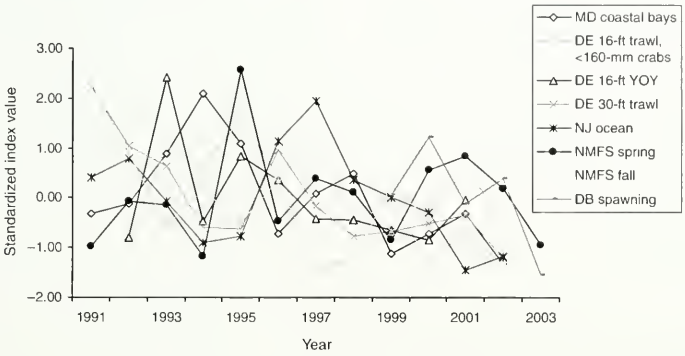

Figure 1

Fishery-independent survey indices for the Delaware Bay (DB) region from 1991 through 2003, standardized by survey for comparison. MD = Maryland; DE = Delaware; NJ = New Jersey; DB=Delaware Bay.

$$\frac{dB_t}{d_t} = (r - F_t)B_t - \frac{rB_t^2}{K},$$

where r = the stock's intrinsic growth rate;
K = the carrying capacity, both of which are assumed to be constant (Prager, 1994); and
F_t and B_t = Fishing mortality and biomass, respectively, at time t.

In addition, the harvest was not assumed to equal surplus production (i.e., the model was a dynamic or non-equilibrium model; Quinn and Deriso, 1999). This model assumes $B_{MSY} = 0.5K$, where B_{MSY} is the spawning biomass that would produce MSY. This form is often used because of its theoretical simplicity and because it is central among possible production model shapes. This production model was conditioned on catch, meaning that landings data were assumed to be more precise than abundance indices. By assuming that abundance indices are correlated measures of population abundance, the model is able to incorporate multiple indices by interpreting differences among indices as sampling error. To fit the production model, we used the ASPIC software (vers. 5.02) of Prager (1994), a program that has been used extensively in stock assessments (Cadrin and Hatfield, 2002; MacCall, 2002). We included data from fishery-independent and fishery-dependent sources in model runs.

Abundance indices

In the Delaware Bay region, there are a number of fishery-independent surveys that collect data on horseshoe crabs (Fig. 1). These include National Marine Fisheries Service (NMFS) trawl (spring, 1968–2003, and fall, 1963–2002), New Jersey (NJ) ocean trawl (1989–2002), Maryland (MD) coastal bays trawl (1988–2002), Delaware (DE) 16-ft trawl (juvenile and young-of-the-year; 1992–2002), DE 30-ft trawl (1990–2002), and Delaware Bay spawning survey (1999–2003). Detailed descriptions of these surveys can be found in ASMFC.[2] We selected 1991–2003 as the modeling timeframe because both harvest data and abundance index data were available for this period.

In spite of the large number of surveys and long time series for some of these surveys, many had high variability and low power to detect a decline. Additionally, many of these surveys were negatively correlated with each other for the years investigated (Table 1). Because an underlying assumption for the model is that each survey is representative of the population being evaluated, total disagreement (i.e., negative correlation) among any pair of surveys cannot be reconciled by the model, resulting in model errors. We therefore used three subsets of fishery-independent surveys in which all pairs were positively correlated for population modeling (Table 2), incorporating six of the eight fishery-independent surveys into production model runs. Fishery-dependent data were also available from 1991 to 2002 from the Delaware hand and dredge fisheries. Abundance indices based on catch-per-unit-of-effort (CPUE) for these fisheries were calculated from the annual number of trips and landings for each fishery (Fig. 2).

Within the models, abundance indices were weighted by the inverse of the coefficient of variation (CV) from regressions, which gave more weight to surveys with less variability. For comparison, we also conducted model

runs where surveys were weighted equally within the models. Table 2 lists the three fishery-independent models (referred to as FI) and the four fishery-dependent models (referred to as FD) used in production model applications and the CV and weighting of each survey within the models.

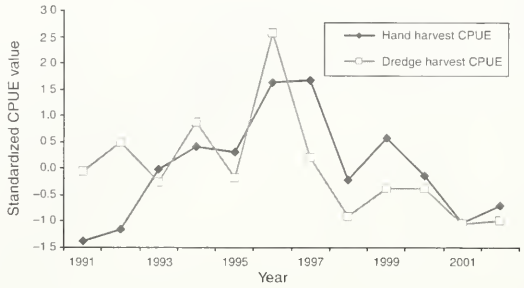

Figure 2

Fishery-dependent abundance indices based on catch-per-unit-of-effort data for the Delaware hand and dredge horseshoe crab (*Limulus polyphemus*) fisheries, 1991–2002, standardized by index for comparison.

Harvest

We obtained horseshoe crab harvest data for Virginia, Maryland, Delaware, Pennsylvania, and New Jersey from 1995 to 2003 (NMFS[7]; Michels[8]). We combined harvests among states for regional-scale production model runs. We estimated the regional harvest from 1991 to 1994 from available Delaware landings data (Fig. 3). Reporting of harvest was not mandatory during this time period, and harvest data

[7] NMFS (National Marine Fisheries Service). 2004. Fisheries Statistics and Economics Division, Silver Spring, MD. Landings data (by state and year) obtained in August 2004 from http://www.st.nmfs.gov/st1/commercial/index.html. Web page was last modified 24 September 2003.

[8] Michels, S. Personal commun. 2004. DE Div. of Fish and Wildlife, 89 Kings Highway, Dover, DE 19901.

Table 1

Correlation matrix for abundance indices derived from 10 surveys, with number of pairwise comparisons (i.e., years) in parentheses for 1991–2003. Negatively correlated indices are shown in bold font. Indices used in production model runs are identified with an asterisk (*).

		1 NMFS fall	2 NMFS spring	3 DE 30-ft trawl	4 DE 16-ft trawl, <160-mm crabs	5 DE 16-ft trawl, YOY	6 NJ ocean	7 MD coast	8 Spawning survey	9 DE dredge	10 DE hand
1	NMFS sall	1.000 (12)									
2	NMFS spring*	**−0.409** (12)	1.000 (13)								
3	DE 30-ft* trawl	0.706 (12)	**−0.370** (12)	1.000 (12)							
4	DE 16-ft trawl, <160-mm* crabs	**−0.261** (11)	0.182 (11)	0.215 (11)	1.000 (11)						
5	DE 16-ft trawl, YOY*	**−0.153** (10)	0.214 (10)	0.341 (10)	0.617 (10)	1.000 (10)					
6	NJ ocean*	**−0.102** (12)	**−0.249** (12)	0.479 (12)	0.252 (11)	**−0.132** (10)	1.000 (12)				
7	MD coastal bays*	**−0.181** (12)	0.086 (12)	**−0.038** (12)	0.639 (11)	0.336 (10)	**−0.116** (12)	1.000 (12)			
8	Spawning survey	**−0.786** (4)	0.211 (5)	**−0.069** (4)	**−0.657** (4)	**−0.781** (3)	0.392 (4)	**−0.087** (4)	1.000 (5)		
9	DE dredge harvest*	0.210 (12)	**−0.329** (12)	0.450 (12)	0.379 (11)	0.031 (10)	0.506 (12)	0.135 (12)	0.509 (4)	1.000 (12)	
10	DE hand harvest	**−0.536** (12)	0.002 (12)	**−0.214** (12)	0.639 (11)	0.084 (10)	0.485 (12)	0.123 (12)	0.167 (4)	0.564 (12)	1.000 (12)

from other states were unavailable or unreliable. We therefore expanded the Delaware harvest to represent the Delaware Bay region by making the assumption that regional landings were equal to ten times the landings in Delaware, the approximate relationship from 1997 through 2003 when reporting was mandatory. When applicable, we converted numbers to metric tons (t) (Prager and Goodyear, 2001) using the relationship of Gibson and Olszewski[6] (1.8182 kg/horseshoe crab). Commercial harvest of horseshoe crabs has been below the regional quota of 2595 t since 2000 (Fig. 3).

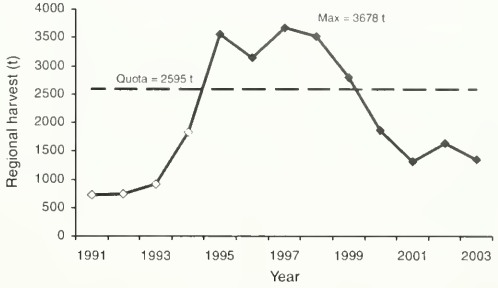

Figure 3

Delaware Bay regional horseshoe crab (*Limulus polyphemus*) harvest (in t). Regional harvest, 1991–1994 (open diamonds), was estimated to be ten times the Delaware harvest. The current regional quota of 2595 t is shown by the horizontal line.

Assumptions associated with the production models

There were a number of general assumptions associated with production models (Quinn and Deriso, 1999). We assumed that productivity (change in biomass over time) responded instantaneously to changes in population size. Changes in the biotic and abiotic environments were ignored, and r (the intrinsic rate of population growth) and K (the carrying capacity) were assumed to be constant. Because production models combine all age classes, it was assumed that size or age structure of the population would not have major effects on population dynamics.

Specific assumptions about population values were also required by the model. All starting values of MSY and K were based on the maximum harvest in the Delaware Bay from 1991 through 2003. The initial guess for MSY was 1850 t (half of the largest catch), and the initial guess for K was 37,000 t (ten times the largest catch). For fishery-independent model runs, we had the model freely estimate initial biomass in relation to carrying capacity (B_1/K), with our start-

Table 2

Description of production model runs, including the data sources, years, and coefficient of variation (CV) from regression analyses. The weighting of surveys within the models is the inverse of the CV. The starting estimate of B_1/K for each model is also shown. FI refers to models that include fishery-independent abundance indices, and FD identifies models where fishery-dependent indices from CPUE data were used.

Model	Data sources	Years	CV	Relative weighting	Initial B_1/K value
FI-1	NMFS spring	1991–2003	0.636	0.241	0.5
	DE 16-ft trawl, <160-mm crabs	1992–2002	0.517	0.296	
	DE 16-ft trawl YOY	1992–2001	0.928	0.165	
	MD coastal bays	1991–2002	0.515	0.297	
FI-2	DE 30-ft trawl	1991–2002	0.524	0.388	0.5
	DE 16-ft trawl, <160-mm crabs	1992–2002	0.517	0.393	
	DE 16-ft YOY	1992–2001	0.928	0.219	
FI-3	DE 30-ft	1991–2002	0.524	0.283	0.5
	DE 16-ft trawl, <160-mm crabs	1992–2002	0.517	0.287	
	NJ ocean trawl	1991–2002	0.345	0.430	
FD-1	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.1
	DE dredge CPUE	1991–2002	0.555	0.447	
FD-2	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.2
	DE dredge CPUE	1991–2002	0.555	0.447	
FD-3	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.3
	DE dredge CPUE	1991–2002	0.555	0.447	
FD-4	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.4
	DE dredge CPUE	1991–2002	0.555	0.447	

ing estimate of this value equal to 0.5. In the absence of other information about starting biomass, B_1/K = 0.5 (i.e., B_1=B_{MSY}) is an appropriate default value (Punt, 1990; Prager, 1994). In some cases B_1/K was poorly estimated, and we employed a common solution of fixing the value of B_1/K (Vaughan and Prager, 2002). For model runs based on fishery-dependent indices, we fixed B_1/K at 0.1, 0.2, 0.3, and 0.4 (Table 2). The CPUE value for the Delaware hand fishery was relatively low in 1991; therefore we assumed that the population biomass was below B_{MSY}, i.e. B_1/K was less than 0.5.

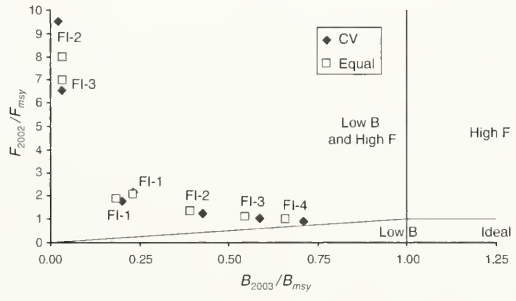

Figure 4

Relative 2003 biomass (B_{2003}/B_{MSY}) and relative 2002 fishing mortality (F_{2002}/F_{MSY}) of Delaware Bay horseshoe crab (*Limulus polyphemus*) for each of the seven model runs presented, with abundance indices weighted equally or inversely to CV within the models.

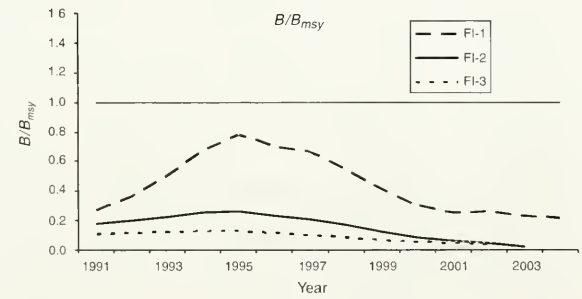

Figure 5

Production model estimates of relative biomass (B/B_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2004. Results from fishery-independent model runs are shown, and the horizontal line represents B/B_{MSY}=1. 80% confidence intervals each model run are the same line pattern in gray.

Quantities estimated by the model

The production model estimated several benchmarks and status indicators useful in understanding horseshoe crab biology and in improving management. These quantities included relative biomass (B/B_{MSY}), relative fishing mortality (F/F_{MSY}), population biomass (B), and maximum sustainable yield (MSY). Point estimates and 80% confidence intervals for each of these quantities were calculated for each model run.

Population projections

We used the Delaware Bay population estimates calculated by the surplus production model to project the population forward in time for a period of 15 years to evaluate potential harvest levels. We conducted projections using ASPICP (Prager, 1994), with annual landings specified for each year of the projections. We selected a 15-year time period because this is the longest projection period that can be programed in ASPICP, and confidence in projection model results decreases at longer time intervals. We evaluated trends in biomass over time for a range of harvest levels, including harvest at 2003 levels and proportional reductions of that harvest. These harvests were 0% of 2003 catch (no harvest), 25% (339 t annually), 50% (678 t), 75% (1017 t), and 100% (1356 t). We identified the number of years under each harvest scenario required for the population (and 80% confidence intervals) to rebuild to B_{MSY}. We also compared relative biomass (with 80% confidence intervals) in the final year of projections (2018) for each harvest level.

Results

Results differed little between model simulations for surveys weighted inversely to CV and for simulations with equally weighted surveys (Fig. 4).

B/B_{MSY}

Production model runs showed that B/B_{MSY} in the Delaware Bay region increased in the early 1990s and has declined steadily since 1995 (Figs. 5 and 6). Slight increases since 2001 were evident in some model runs. Relative biomass in 2003 was estimated to be low, with point estimates ranging from 0.03 to 0.20 for models with fishery-independent data and 0.20 to 0.71 for models with fishery-dependent data (Table 3). Eighty-percent confidence intervals for B_{2003}/B_{MSY} ranged from 0.005 to 1.16.

Table 3

Status indicators and management benchmarks for horseshoe crabs in the Delaware Bay region, estimated from production model runs with fishery-independent (FI) or fishery-dependent (FD) indices weighted by the inverse of the CV. Point estimates and lower (L) and upper (U) 80% confidence intervals (CIs) are shown for each model run. The objective function is a measure of how well the model was able to fit the data using a lognormal error structure—a lower value representing a better fit.

	FI-1	FI-2	FI-3	FD-1	FD-2	FD-3	FD-4
B_{2003}/B_{MSY}	0.232	0.022	0.030	0.201	0.427	0.588	0.710
80% CI (L)	0.109	0.005	0.008	0.127	0.238	0.319	0.388
80% CI (U)	0.479	0.154	0.041	0.347	0.762	1.015	1.157
F_{2002}/F_{MSY}	2.156	9.501	6.560	1.795	1.269	1.034	0.911
80% CI (L)	1.442	6.005	3.999	1.258	0.770	0.588	0.513
80% CI (U)	3.299	18.320	21.300	2.592	2.069	2.112	2.184
B_{2003} (t)	2197	1084	4098	2579	3653	5035	6604
80% CI (L)	1319	524	2295	1423	1853	2955	4340
80% CI (U)	4603	4306	9379	4372	5012	7778	12,080
MSY (t)	3064	5082	7220	3768	2628	2354	2196
80% CI (L)	2550	2985	5340	3274	2566	1905	1372
80% CI (U)	4475	8713	9577	4499	2787	2505	2501
Objective function	16.05	12.40	9.57	2.62	2.93	3.39	3.85

F/F_{MSY}

Although harvest of horseshoe crabs has decreased in recent years (Fig. 3), fishing mortality remains high (Figs. 7 and 8). F_{2002}/F_{MSY} point estimates ranged from 2.3 to 9.5 for models with fishery-independent data and from 0.9 to 1.8 for models with fishery-dependent data (Table 3).

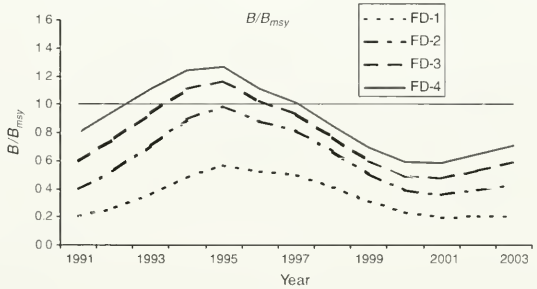

Figure 6

Production model estimates of relative biomass (B/B_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2003. Results from fishery-dependent model runs are shown, and the horizontal line represents B/B_{MSY}=1. 80% confidence intervals for models FD-1 and FD-4 are shown in gray.

Biomass

Biomass of horseshoe crabs in the Delaware Bay region has decreased substantially since 1995, such that the 2003 biomass was less than 56% of the 1995 biomass. This equates to an annual decline of greater than 7% during this period. Point estimates for 2003 biomass ranged from 1084 t (596,000 crabs) to 6604 t (3,632,000 crabs). As is characteristic of production models (Prager, 1994), absolute biomass was estimated much less precisely than relative biomass (B/B_{MSY}). The range of 80% confidence intervals for 2003 biomass across all seven model runs was 524 t (288,000 crabs) to 12,080 t (6,644,000 crabs).

Population projections

We used results from production model runs to project the horseshoe crab population forward in time to evaluate potential management options. Figure 9 shows the trajectory of B/B_{MSY} over time for model FI-1 under each harvest scenario. The number of years required to rebuild the population to B_{MSY} varied substantially among models (Table 4). At 2003 harvest levels (i.e., 100%), projections showed population recovery in a minimum of four years, although four of the seven models did not reach B_{MSY} in the 15-year projection period. In the absence of harvest (i.e., 0%), recovery could occur in as few as 2 years, but two models did not reach B_{MSY} in the projection period. Estimates of B/B_{MSY} in the final year of projections (2018) also differed among model applications (Table 5).

Discussion

According to surplus production model runs and corresponding projections, the horseshoe crab population in the Delaware Bay region has been depleted and current harvest levels may be too high to allow the population to rebuild to B_{MSY} within 15 years. Biomass in this region has decreased steadily since 1995 and is currently well below B_{MSY}. This decline was evident in models that incorporated regional fishery-independent surveys and Delaware fishery-dependent indices. Figure 4 shows current relative biomass and relative fishing mortality for each of the model applications. All model runs indicated a depleted population with high fishing mortality, although the estimated extent differed among models (Fig. 4). Projections for some of the model runs predicted a relatively fast population recovery. In the absence of harvest, five of the seven model applications predicted rebuilding to B_{MSY} in five or fewer years. However, two of the model runs estimated such low population biomass that rebuilding the Delaware Bay population to B_{MSY} would take greater than 15 years, even with no harvest. A precautionary management strategy may therefore be appropriate for this population in the short term as more data are being collected.

Population model results may have been affected by assumptions that we made during the modeling process. In order to extend the time period of the model back to 1991, we had to estimate regional harvest based on Delaware harvest data for the early years of the model. Because harvest data from most states were not available prior to 1995, we assumed that regional harvest was equal to ten times the Delaware harvest for the years 1991–94. This was the approximate relationship between Delaware and regional harvest from 1997 through 2003 when reporting was mandatory. Actual regional harvest for 1991–94 was unknown because there were no harvest-reporting requirements. We conducted sensitivity analyses which showed very little difference among runs with 1991–94 harvest equal to Delaware landings, 10 times Delaware landings, or 20 times the Delaware landings (the mean difference for B_{2003}/B_{MSY} from these runs was 0.011). If the actual harvest was substantially greater than 20 times Delaware landings, differences in results may occur.

Results were also influenced by the data sources that were included. We based the inclusion of fishery-independent surveys on positive correlations among surveys, incorporating the largest number of data sources possible into model runs. However, two fishery-independent surveys were not included: the NMFS fall trawl and the Delaware Bay spawning survey. The NMFS fall trawl was negatively correlated with seven of the nine other data sources (Table 1), and we therefore assumed that it was not a reliable index of horseshoe crab abundance. The spawning survey was negatively correlated with five of the nine other data sources (Table 1). This survey also had a very short time series because it was redesigned in 1999 to improve statistical power (Smith et al., 2002). With so few data points, the production model would be unable to distinguish population trends from survey variability; therefore spawning survey data were excluded. However, as one of only two horseshoe crab-specific surveys currently in place, the Delaware Bay spawn-

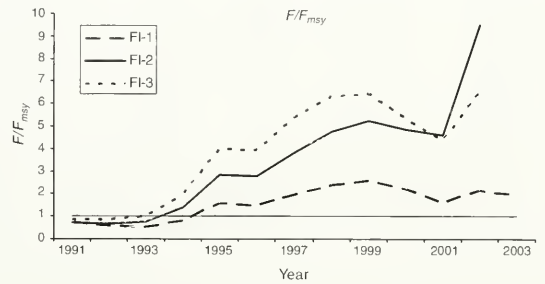

Figure 7

Production model estimates of relative fishing mortality (F/F_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2003. Results from fishery-independent model runs are shown, and the horizontal line represents F/F_{MSY}=1. 80% confidence intervals for each model run are the same line pattern in gray.

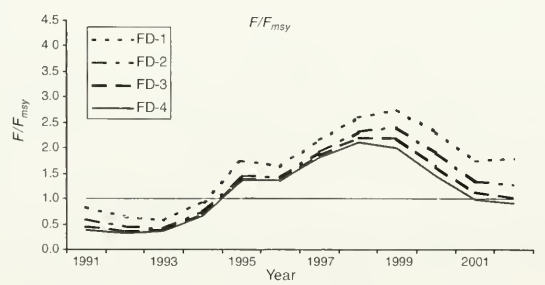

Figure 8

Production model estimates of relative fishing mortality (F/F_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2002. Results from fishery-dependent model runs are shown, and the horizontal line represents F/F_{MSY}=1. 80% confidence intervals for models FD-1 and FD-4 are shown in gray.

ing survey will likely prove to be a valuable source of information in the future.

Negative correlations were present among a relatively large number of Delaware Bay surveys (Table 1) which are assumed to be sampling the same population. This is a common problem in fisheries stock assessments (Richards, 1991; Schnute and Hilborn, 1993). The observed differences among these surveys could be attributed to a number of factors. Catches of horseshoe crabs are not common, leading to small sample sizes and high variability. Also, these surveys may differ in location, time of year, and gear selectivity. Future studies could employ an analysis of variance (ANOVA) to attempt to separate these factors from underlying horseshoe crab abundance trends.

The data sources included in individual model runs also led to differing results. Models incorporating fishery-dependent data tended to present a slightly more optimistic view of the population and the fishery, predicting higher relative biomass and lower relative fishing mortality. Although harvest data often have the benefit of having been derived from large sample sizes (and have resulting low variance estimates), there is often a bias associated with fishery-dependent data. Fisheries do not sample randomly because they target areas of highest abundance, and thus biased indices are produced (Quinn and Deriso, 1999). In addition, the use of fishery-dependent abundance indices is often complicated by changes in gear, regulations, or sampling methods over time, any of which could affect catch rates. Fishery-independent surveys are usually more appropriate for assessments, assuming there is high consistency in sampling methods among years (Chen et al., 2003).

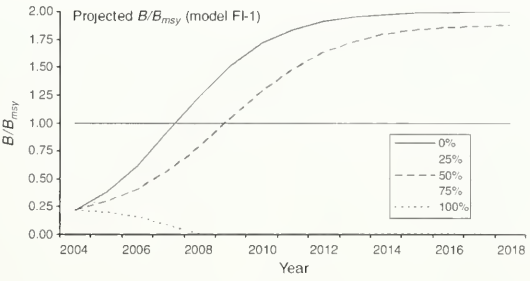

Figure 9

Example of projection results. Projected relative biomass (B/B_{MSY}) in shown for model FI-1, with each line representing a harvest level applied annually in the 15-year projections. The percentage refers to the percent of the 2003 Delaware Bay regional landings of 1356 t (i.e., 50% = 678 t).

Differences also existed among fishery-independent surveys. Models FI-2 and FI-3 predicted a much lower population size than FI-1 or the fishery-dependent models. Projections with these runs predicted that the population was too depleted to recover in 15 years, even in the absence of harvest. The models differed only in the abundance indices included. In the trend analyses conducted for ASMFC,[2] the most significant population declines since 1997 were identified in the NJ ocean

Table 4

Results of Delaware Bay population projections from production model runs from fishery-independent (FI) and fishery-dependent (FD) indices. Projections were conducted for 15 years, with a constant harvest (in t) applied annually. Harvest levels were based on 2003 harvest and are listed in the left column. The time period (and 80% confidence intervals) shown represent the number of years (starting in 2003) required for the population biomass to reach B_{MSY}. "n/a" indicates that the biomass did not reach B_{MSY} during the 15-year projection period.

Harvest level in relation to that of 2003	Years to rebuild to B_{MSY}						
	FI-1	FI-2	FI-3	FD-1	FD-2	FD-3	FD-4
0% (0 t)	5 years	n/a	n/a	4 years	3 years	2 years	2 years
80% CI	(2, 12)	(3, n/a)	(n/a, n/a)	(3, 7)	(1, 6)	(0, 8)	(0, 15)
25% (339 t)	5	n/a	n/a	5	3	2	2
80% CI	(2, n/a)	(3, n/a)	(n/a, n/a)	(3, 8)	(1, 8)	(0, 9)	(0, n/a)
50% (678 t)	6	n/a	n/a	6	4	3	2
80% CI	(2, n/a)	(n/a, n/a)	(8, n/a)	(3, 11)	(1, 10)	(0, 14)	(0, n/a)
75% (1017 t)	9	n/a	n/a	7	4	3	3
80% CI	(3, n/a)	(n/a, n/a)	(5, n/a)	(4, 15)	(1, n/a)	(0, n/a)	(0, n/a)
100% (1356 t)	n/a	n/a	n/a	n/a	6	5	4
80% CI	(3, n/a)	(n/a, n/a)	(n/a, n/a)	(5, n/a)	(2, n/a)	(0, n/a)	(0, n/a)

Table 5

Results of Delaware Bay population projections from production model runs from fishery-independent (FI) and fishery-dependent (FD) indices. Projections were conducted for 15 years, with a constant harvest (in t) applied annually. Harvest levels were based on 2003 harvest and are listed in the left column. The relative biomass (B/B_{MSY}) in the final year of projections (2018) and 80% confidence intervals are shown for each model simulation.

Harvest level in relation to that of 2003	B_{2018}/B_{MSY}						
	FI-1	FI-2	FI-3	FD-1	FD-2	FD-3	FD-4
0% (0 t)	2.00	0.41	0.14	2.00	2.00	2.00	2.00
80% CI (L)	1.49	0.02	0.04	1.91	1.87	1.63	1.05
80% CI (U)	2.00	1.97	0.28	2.00	2.00	2.00	2.00
25% (339 t)	1.94	0.00	0.06	1.95	1.93	1.92	1.91
80% CI (L)	0.00	0.00	0.00	1.95	1.90	1.42	0.86
80% CI (U)	1.96	1.94	0.42	1.95	1.93	1.93	1.93
50% (678 t)	1.87	0.00	0.00	1.90	1.86	1.84	1.82
80% CI (L)	0.00	0.00	0.00	1.89	1.80	1.07	0.61
80% CI (U)	1.93	0.00	1.76	1.90	1.86	1.86	1.86
75% (1017 t)	1.78	0.00	0.00	1.83	1.78	1.74	1.71
80% CI (L)	0.00	0.00	0.00	1.66	0.86	0.57	0.26
80% CI (U)	1.85	0.00	1.74	1.85	1.78	1.78	1.77
100% (1356 t)	0.00	0.00	0.00	0.76	1.67	1.62	1.58
80% CI (L)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
80% CI (U)	1.72	0.00	0.00	1.77	1.69	1.69	1.68

trawl and the DE 16-ft 160-mm survey, both of which were included in model FI-3, and possibly explain the low population estimates.

In other trend analyses conducted during the previous assessment, a population decline in the Delaware Bay was less evident. Using data from 1997 through 2003, we found that only four of eight fishery-independent surveys showed a significant decline, partially owing to high variability and low power. By incorporating a number of these surveys into a production model, we also found that the decreasing biomass in recent years becomes more apparent. These production model runs provide the added benefit of estimating stock status and management benchmarks, as well as the benefit of evaluating future management options.

Although interpretation of absolute biomass or population size from a surplus production model can be somewhat problematic, our estimates are roughly comparable to estimates from previous studies. Hata and Berkson (2003) calculated a mean 2001 population size of 4.4 million adults (95% confidence intervals of 2.1 million and 6.8 million) in the Delaware Bay from daytime trawl survey data. Botton and Ropes (1987) estimated 2.3 to 4.5 million adults in this region. In the present study, our estimates of the 2003 population size ranged from 0.6 million to 3.6 million crabs, and the mean of the seven model runs equaled 2.0 million crabs. Eighty percent confidence intervals ranged from 0.3 million to 6.6 million crabs for all model applications. Although within the range of results from the other studies, these wide confidence intervals provide little information for management. It will therefore be more appropriate to interpret relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}) for use in management decisions (Prager, 1994).

It is important to understand the spatial scale and population represented by these models and analyses. This regional model is a compilation of a number of localized fishery-independent surveys, most of which encompassed a relatively small spatial area. However, the model results should not be interpreted at a more localized scale because landings data are combined for the region. Similarly, interpretation of results should not be expanded to represent other Atlantic horseshoe crab populations outside the Delaware Bay region because neither survey nor harvest data in this model extend to other regions. Nevertheless, the Delaware Bay is believed to be the center of abundance and spawning activity for Atlantic horseshoe crabs; therefore population trends in this region may have significant implications for adjacent populations.

In analyses conducted for ASMFC,[2] trend analyses identified dramatic regional differences in horseshoe crab population trends. Although the Delaware Bay, eastern Long Island Sound, and New England populations have experienced declines in recent years, the southeast population and the western Long Island population have remained stable or have increased. Future production models applied to these other regions will hopefully clarify these trends and allow managers to

determine regional harvest regulations. By identifying appropriate management for each region, we will improve our ability to rebuild the Atlantic horseshoe crab population and provide a sustainable resource for the diverse user groups.

Acknowledgments

This research was funded by the National Marine Fisheries Service. We thank M. Prager and M. Gibson for providing modeling advice, D. Smith, S. Michels, and B. Andres for providing horseshoe crab data and guidance, and the members of the Horseshoe Crab Stock Assessment and Technical Committees of the ASMFC for their contribution to this study. This manuscript was improved by the comments and suggestions from M. Prager, M. Millard, S. Michels, B. Murphy, D. Hata, and S. Klopfer, and two anonymous reviewers. We greatly appreciate the time and effort of all involved.

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Biodiversity as an index of regime shift in the eastern Bering Sea

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Abstract—Data collected from an annual groundfish survey of the eastern Bering Sea shelf from 1975 to 2002 were used to estimate biomass and biodiversity indexes for two fish guilds: flatfish and roundfish. Biomass estimates indicated that several species of flatfish (particularly rock sole, arrowtooth flounder, and flathead sole), several large sculpins (*Myoxocephalus* spp.), bigmouth (*Hemitripterus bolini*), and skates (*Bathyraja* spp.) had increased. Declining species included several flatfish species and many smaller roundfish species of sculpins, eelpouts (*Lycodes* spp.), and sablefish (*Anoplopoma fimbria*). Biodiversity indexes were calculated by using biomass estimates for both guilds from 1975 through 2002 within three physical domains on the eastern Bering Sea shelf. Biodiversity trends were found to be generally declining within the roundfish guild and generally increasing within the flatfish guild and varied between inner, middle, and outer shelf domains. The trends in biodiversity indexes from this study correlated strongly with the regime shift reported for the late 1970s and 1980s.

Manuscript submitted 25 March 2004 to the Scientific Editor's Office.
Manuscript approved for publication 13 August 2005 by the Scientific Editor.
Fish. Bull. 104:226–237 (2006).

Environmental and biological events in the North Pacific can indicate regime shifts or reorganizations of the ecosystem at the environmental and biological level (Hare and Mantua, 2000). Measurable climatic events were identified in the mid-1970s, late 1980s (Anderson and Piatt, 1999; Anderson, 2000; Hare and Mantua, 2000; Zhang et al., 2000; Minobe, 2002) and the late 1990s (Hunt and Stabeno, 2002; Minobe, 2002). Regime shifts in the eastern Bering Sea (EBS) have been correlated with several climatic events, including the Pacific Decadal Oscillation, the El Niño Southern Oscillation (Hollowed et al., 2001), sea ice coverage (Stabeno et al., 2001; Hunt et al., 2002; Hunt and Stabeno, 2002), and summer sea surface temperatures (Bond and Adams, 2002; Hunt et al., 2002; Minobe, 2002). The far reaching effects that climate change has on an ecosystem are not well defined, but many studies have shown strong correlations between climate change, fish recruitment, and plankton production in the North Pacific (Brodeur and Ware, 1992; Anderson et al., 1997; Anderson and Piatt, 1999; Brodeur et al., 1999; Clark et. al., 1999; Hare and Mantua, 2000; Zhang et al., 2000; Hollowed et al., 2001; Sugimoto et al., 2001; Conners et al., 2002; Hunt et al., 2002; Wilderbuer et al., 2002). During periods of climatic change, some fishes may not be well adapted to dramatic changes over a short time scale (1–10 years), whereas others may proliferate in a more hospitable environment. Key triggers of regime shifts and the extent to which species will respond remain unclear; however, evidence may indicate that species diversity is correlated with primary production in many systems, and the two may be interdependent (Rosenzweig and Abramsky, 1993; Waide et al., 1999). A biodiversity index can be useful for monitoring the stability, health, and productivity of an ecosystem, as well as for aiding management, by tracking exogenous changes and their far reaching effects on species. In the present study, I used biodiversity indexes, reflecting richness and evenness, as indicators of species composition changes and related these changes to regime shift events for the eastern Bering Sea (EBS) shelf.

Methods

Data were synthesized from a continuous 24-year period of standardized groundfish surveys conducted by the Alaska Fisheries Science Center (AFSC) on the EBS shelf from 1979 through 2002; additional estimates from 1975 were included. Biodiversity indexes (species richness and evenness) were calculated from biomass estimates for two fish guilds, flatfish and roundfish, in each of the inner, middle, and outer domains of the EBS shelf. Biodiversity indexes were plotted for each fish group and domains and examined for changes over the study period. The observed changes were correlated with regime shift and ocean climatic change events for the EBS.

Data collection

Gear, station location, sampling procedures, and time of year of the AFSC

eastern Bering Sea continental shelf survey have been standardized since 1982. Prior to 1982, a 400-mesh eastern trawl (smaller than the current 83-112 trawl) was used (Bakkala, 1993). Although the biomass estimates produced by the two trawls are not directly comparable because of unknown catchability differences between the nets, survey data from 1975 and 1979–81 were included in the present analysis because of the importance in the timing of the 1970s regime shift. The biodiversity indexes are based on the relative proportion of the species and therefore are an indicator of assemblage structure.

Data used for this study were collected by the Resource Assessment and Conservation Engineering (RACE) division of the AFSC, which surveys the EBS shelf each summer (May–August). The survey area extends from the Alaska Peninsula north to Nunivak Island and St. Matthew Island, and west to the 200 m shelf break. Trawl hauls were conducted on a grid of 356 fixed stations (20 nmi by 20 nmi) (Fig. 1) during daylight hours. Hauls were towed for 30 min at 3 knots and ranged in depth from 15 m in Bristol Bay to nearly 200 m near the shelf edge. Most trawling was conducted with the AFSC 83-112 eastern trawl (1982–2002), which is a low-opening two-seam trawl with a 26.5-m headrope and 34.1-m cable footrope wrapped with rubber striping and chain hangings that contact the bottom while the trawl is towed (Rose and Walters, 1990).

Height and width of the net were measured with an acoustic SCANMAR (Scanmar, Asgardstrand, Norway) or NETMIND (Northstar Technical Inc., St. John's, NF, Canada) net mensuration system, or estimated by using a function that relates trawl widths to tow depths from measured hauls. Each haul was measured with GPS or LORAN to record latitude and longitude data at the start and end of the trawl in order to determine distance fished.

Processing of the catch was done entirely in the field at the time of capture. The entire catch was sorted to species, enumerated, and weighed, or a weighed subsample was used for very large catches.

Catch per unit of area (CPUE) was determined for each trawl station completed during each survey. Biomass estimates for each species were then calculated by expanding the average CPUE for each stratum and then summing over all strata of the total survey area to obtain a biomass estimate in metric tons for each species.

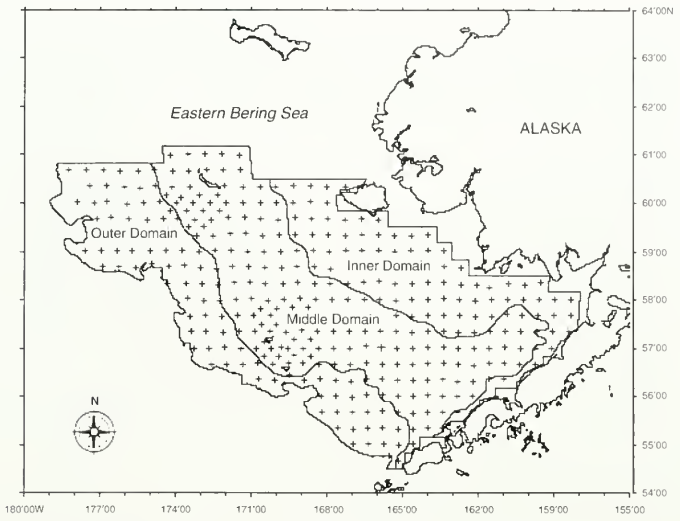


Figure 1

Survey area in the eastern Bering Sea. Crosses represent annual trawl survey stations from 20–200 m. Bathymetry lines delineate the inner, middle and outer domains.

EBS shelf domains and study area

The EBS is composed of three well-defined regions designated as the inner, middle, and outer domains from east to west, respectively, across the shelf (Fig. 1). The three domains are distinct regions characterized by depth, water temperature, current flow, summertime primary production, and species composition (Bakkala, 1993; Schumacher and Stabeno, 1998; Stabeno et al., 2001). Briefly, the inner domain is a relatively shallow (<50 m) and well-mixed warm basin with strong influences from a large coastal area, several major river systems, and a current flow northward along the coast from the Aleutian Islands. The middle domain is a relatively stagnant area of deeper water (50–100 m) that has strong summer water-column stratification and low current flows. The bottom water mass is relatively cold, overlaid by a layer of warmer wind-mixed water. Although characterized as a cold region, the water mass in the middle domain varies from year to year. The outer domain is influenced by the EBS slope region and by upwelling and northward current flow from the Aleutian Islands. This domain is relatively warm when compared to the middle domain (see Hunt et al., 2002, for review). For the purposes of this study the inner domain designation consisted of trawl stations less than 50 m in depth; the middle shelf designation was for trawl stations between 51 and 100 m in depth; and outer domain designation was for trawl stations between 101 and 200 m in depth.

Table 1

Flatfish guild species or species groups used for biodiversity indexes. * indicates the major proportion of the biomass for the group. Superscripts indicate the primary domains where each species occurs during the summertime AFSC survey. I=inner domain, M=middle domain, O=outer domain.

Group name	Scientific name
Pacific halibut	*Hippoglossus stenolepis*^{IMO}
Flathead/Bering flounder	**Hippoglossoides elassodon* and *H. robustus*^{IMO}
Greenland turbot	*Reinhardtius hippoglossoides*^{O}
Arrowtooth/Kamchatka flounders	**Atheresthes stomias* and *A. evermanii*^{MO}
Starry flounder	*Platichthys stellatus*^{IM}
Alaska plaice	*Pleuronectes quadrituberculatus*^{IM}
Northern/southern rock sole	**Lepidopsetta polyxystra* and *L. bilineata*^{IMO}
Longhead dab	*Limanda proboscidea*^{I}
Yellowfin sole	*Limanda aspera*^{IM}
Rex sole	*Glyptocephalus zachirus*^{O}
Oher flatfish	**Isopsetta isolepis*^{IM}, **Limanda sakhalinensis*^{MO}, *Psettichthys melanostictus, Microstomus pacificus*

Fish assemblages differed noticeably among the inner, middle, and outer domains in the EBS; many species (sculpins, poachers, and eelpouts) primarily inhabited a single domain and many flatfishes and skates inhabited all three domains (Kaimmer[1]; Kinder and Schumacher, 1981; Smith and Bakkala, 1982: Tables 1 and 2). Because of the distinct domain environments and assemblages, the flatfish and roundfish species groups were analyzed by inner, middle, and outer domains separately and all domains were combined to detect the influence of climate change on each assemblage.

Species groups

The taxonomic level of species identification for the entire survey period (1975–2002) has varied because of an incomplete knowledge of species characters and because of survey time constraints at-sea. Historically, survey goals were to obtain fisheries data on commercially or potentially commercially important species, and limited effort was put forth for identification of other species. However, given more efficient technologies, better identification field guides, and increased focus on noncommercial species, species identification has improved and is approaching the current extent of taxonomic knowledge.

Efforts in recent years (1998–2002) have increased our knowledge of current species distributions in the EBS shelf region. To assess species-identification confidence over the study period, current species distributions from the AFSC survey and primary literature not associated with AFSC survey data, as well as historical fish collections of selected taxonomic groups (University of Washington Fish Collection, Oregon State University Fish Collection, and Auke Bay Fish Collections) were examined. After this assessment, it was subjectively determined whether species in this study were identified correctly throughout the study period. Species that were determined to be distinguishable and correctly identified were examined as individual species, and species that were possibly misidentified were grouped at a higher taxonomic level for this study. The resulting list of species or species groups includes the greatest number of fish taxa (Tables 1 and 2).

At least 15 flatfish species (within the order Pleuronectiformes) and more than 75 species of fish and elasmobranchs not of the order Pleuronectiformes were recorded during the AFSC summer surveys (1975–2002) on the EBS shelf (20–200 m). Although flatfish make up about 16% of the total number of fish species, they contribute approximately 50% of the biomass of all fish combined (2001 and 2002 AFSC EBS survey estimates). Walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) represent approximately 42% of the survey biomass, and 8% of the biomass that included all other roundfish. Because of the extremely large biomass of walleye pollock and Pacific cod, the biodiversity indexes used are uninformative when walleye pollock and Pacific cod are included owing to the "swamping" effect by their relatively large biomasses when compared to those of other species. To account for this, two species guilds were defined: flatfish and roundfish. The flatfish guild included all Pleuronectiformes recorded from the EBS survey and comprised 11 species or species groups (Table 1). The roundfish

[1] Kaimmer, S. M., J. E. Reeves, D. R., Gunderson, D. R., Smith, G. B., and R. A. Macintosh. 1976. Baseline information from the 1975 OCSEAP survey of the demersal fauna of the eastern Bering Sea. *In* Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975 (W. T Pereyra, J. R. Reeves, and R. G. Bakkala, eds.), p. 157–367. NWAFC Processed Report. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E. Seattle WA 98115.

Table 2

Roundfish guild species or species groups used for biodiversity indexes. * indicates the major proportion of the biomass for the group. Superscripts indicate the primary domains where each species occurs during the summertime AFSC survey. I=inner domain, M=middle domain, O=outer domain. IMO=inner, middle, and outer domains.

Group name	Scientific name
Lamprey	*Lampetra tridentata*
Skate	**Bathyraja parmifera*^{IMO}, **B. interrupta*^{O}, *B. aleutica, B. taranetzi, Raja binoculata*
Shark	**Somniosus pacificus*^{O}, *Squalus acanthias, Lamna ditropis*
Other poachers	**Aspidophoroides bartoni*^{O}, *Bathyagonus alascanus, Leptagonus leptorhynchus, Pallasina barbata, Percis japonicus*
Sawback poacher	*Sarritor frenatus*^{MO}
Sturgeon poacher	*Agonus acipenserinus*^{IM}
Bering poacher	*Ocellus dodecaedron*^{I}
Bering wolffish and wolfeel	*Anarhichas orientalis* and *Anarrhichthys ocellatus*
Searcher	*Bathymaster signatus*^{O}
Other sculpins	*Artedidlus pacificus, Leptocottus armatus, Enophrys* spp., *Psychrolutes paradoxus,Blepsias bilobus, Nautichthys pribilovious, Icelinus* spp.
Staghorn sculpin	**Gymnocanthus pistilliger*^{I}, **G. galeatus*^{O}, *G. detrisus*
Darkfin sculpin	*Malacocottus zonurus*^{O}
Yellow Irish lord	*Hemilepidotus jordani*^{I}
Butterfly sculpin	*Hemilepidotus papilio*^{M}
Triglops sculpins	**Triglops scepticus*^{O}, **T. pingeli*^{IM}, *T. macellus, T. forficatus*
Myoxocephalus sculpins	**Myoxocephalus jaok*^{I}, **M. polyacanthocephalus*^{MO}, *M. verrucosus*^{M}
Spinyhead sculpin	*Dasycottus setiger*^{O}
Bigmouth sculpin	*Hemitripterus bolini*^{O}
Icelus sculpins	**Icelus spiniger*^{O} and **I. spatula*^{IM}
Pacific sandfish	*Trichodon trichodon*^{I}
White-spotted greenling	*Hexagrammos stelleri*^{I}
Snailfish	**Liparis gibbus*^{MO}, **Careproctus rastrinus*^{MO}, *C. cyclospilus*
Smooth lumpsucker	**Aptocyclus ventricosus*^{O}, *Eumicrotremus orbis*
Pricklebacks	**Lumpenus maculata*^{IMO}, **L. sagittae*^{IMO}, *L. fabricii, L. medius, Poroclinus rothrocki*
Other eelpouts	**Lycodes* spp. and *Gymnelus* spp.
Marbled eelpout	*Lycodes raridens*^{I}
Wattled eelpout	*Lycodes palearis*^{MO}
Shortfin eelpout	*Lycodes brevipes*^{O}
Pacific tomcod	*Microgadus proximus*
Saffron cod	*Eleginus gracilis*^{I}
Arctic cod	*Boreogadus saida*^{M}
Pacific sand lance	*Ammodytes hexapterus*
Pacific herring	*Clupea pallasii*^{IM}
Eulachon	*Thaleichthys pacificus*^{O}
Capelin	*Mallotus villosus*^{I}
Rainbow smelt	*Osmerus mordax*^{IMO}
Salmon	*Oncorhynchus* spp.
Sablefish	*Anoplopoma fimbria*^{O}
Atka mackerel	*Pleurogrammus monopterygius*
Prowfish	*Zaprora silenus*^{O}
Rockfish	**Sebastes alutus*^{O}, *S. polyspinis, S. ciliatus*

guild included 40 species or species groups and excluded walleye pollock and Pacific cod (Table 2). The two guilds devised were subjective; however, owing to their distinctive biomass and life history trends, the members of the flatfish guild were examined separately from all other species.

Biodiversity indexes

Biodiversity measures were calculated by using Ludwig and Reynolds's (1988) recommendations for species richness and evenness. Richness and evenness are considered robust measures and allow one to use biomass proportions for biodiversity estimations. The richness index used was as follows:

$$Richness\ index = e^{H'}$$

$$\text{where } H' = \sum_{i=1}^{S}\left[\left(\frac{n_i}{n}\right)\ln\left(\frac{n_i}{n}\right)\right]$$

and n_i = the biomass of individuals belonging to the ith of S species in the sample; and

n = the total summed biomass for the entire guild for a given year (Ludwig and Reynolds, 1988).

The evenness index is the "modified Hill's ratio" (Alatalo, 1981) which is

$$Evenness = \frac{\left(\frac{1}{\lambda}\right)-1}{e^{H'}-1},$$

where $\lambda = -\sum_{i=1}^{S} p_i^2$, where $Pi = \frac{n_i}{N}$ and n_i is the biomass of the ith species and N is the total biomass of all S (species) in the guild (Ludwig and Reynolds, 1988).

Biomass estimates obtained from the surveys were used to calculate biodiversity values for both flatfish and roundfish guilds on an annual basis. Biodiversity values calculated were used as an index of the relative proportion of species in each guild and allowed a direct comparison from year to year of the most abundant species. Species richness indicated the effective number of species that are influencing the index (Hill, 1973; Ludwig and Reynolds, 1988). A higher index indicates a larger number of predominant species in the assemblage (i.e., higher diversity). The evenness index determines the distribution of the biomass proportions of the more abundant species among the species in the guild. As the evenness index approaches zero, the biomass proportion of a single species dominates the guild; as the evenness index approaches one, there is less of a single dominant species and the biomass proportions are shared more equally among many species in the guild (Hill, 1973; Ludwig and Reynolds, 1988).

A piecewise linear model (Neter et al., 1996) was applied to the biodiversity indexes using S-Plus (vers. 6.1, Insightful Corporation, Seattle, WA) to determine distinct breaks or inflection points in the linear data trends. The piecewise model finds a "knot," or inflection point, that breaks the data set into two periods by using the least sum of squared residuals and the highest R^2 for the two-line model to determine the best fit lines to the data. Linear regression models were then applied to the data sets by using the recommended inflection point as the breaking point for the two lines. The years covered for each best fit line, as well as the accompanying linear statistics for the individual lines and the piecewise linear model for the best-fit model are presented in Table 3. The indexes calculated for survey year 1975 are included for reference (denoted as an X on the diversity index graphs) but were not included in the linear regression models because of the time gap from 1975 to 1979 and the lack of confidence in the standardization of the 1975 survey compared with later surveys (Bakkala, 1993).

Results

Flatfish biomass

Biomass estimates for the flatfish guild showed an increase from the late 1970s until the early 1990s, and then an overall slight decline between 1999 and 2002 for all domains (Fig. 2). Species that represented a large portion that showned an increase in biomass estimates over the study period included northern and southern rock sole (*Lepidopsetta polyxystra and L. bilineata,* spp. undetermined), arrowtooth and Kamchatka flounder (*Atheresthes stomias* and *A. evermanni,* spp. undetermined), flathead sole and Bering flounder (*Hippoglossoides elassodon* and *H. robustus,* spp. undetermined), and Pacific halibut (*Hippoglossus stenolepis*). Flatfish species with declining biomass estimates included the yellowfin sole (*Limanda aspera)* and Greenland turbot (*Reinhardtius hippoglossoides*), and a decline in lesser abundant species such as longhead dab (*Limanda proboscidea*) and Alaska plaice (*Pleuronectes quadrituberculatus).* The inner and middle domains were dominated by northern rock sole, yellowfin sole, Alaska plaice, and flathead sole and Bering flounder (spp. undetermined), whereas main portions of the outer shelf comprised arrowtooth and Kamchatka flounder (spp. undetermined), flathead sole and Bering flounder (spp. undetermined), Pacific halibut, and northern and southern rock sole (spp. undetermined).

Roundfish biomass

Roundfish biomass increased from the 1970s to the 1980s and then declined steadily from the early 1990s through 2002 for all domains combined (Fig. 2). Among roundfish species there has been a decline since the 1970s and 1980s in many middle domain species, such as yellow Irish lord (*Hemilepidotus jordani*), butterfly sculpin (*H. papilio*),

Table 3

Statistics of the linear regression models of biodiversity indexes for flatfish and roundfish guilds for the eastern Bering Sea shelf domains. The years encompassing each time period and the piecewise model r^2 for the two-line model are included.

Domain	Index	Years	n	Intercept	Slope	P-value	r^2	Standard error of estimate	r^2 of piecewise model
Flatfish guild									
Inner	Richness	1979–1993	15	−112.9280	0.0579	0.0000	0.8797	0.0993	0.8850
		1994–2002	9	3.9168	−0.0008	0.9645	0.0303	0.1270	
Middle	Richness	1979–1988	10	−358.4240	0.1821	0.0001	0.8829	0.2130	0.8640
		1989–2002	14	7.8482	−0.0020	0.9171	0.0940	0.2887	
Outer	Richness	1979–2002	24	−2.8281	0.0030	0.6875	0.7493	0.2533	
Combined	Richness	1979–1989	11	−327.9090	0.1666	0.0000	0.8740	0.2212	0.9350
		1990–2002	13	6.1232	−0.0012	0.8866	0.1932	0.1150	
Inner	Evenness	1979–1990	12	−48.3712	0.0247	0.0000	0.9291	0.0258	0.9610
		1991–2002	12	−0.0349	0.0005	0.6927	0.0163	0.0161	
Middle	Evenness	1979–1987	9	−61.6390	0.0314	0.0003	0.8663	0.0361	0.8660
		1988–2002	15	3.7805	−0.0015	0.5159	3.3171	0.0375	
Outer	Evenness	1979–2002	24	1.8798	−0.0006	0.6184	0.0115	0.0392	
Combined	Evenness	1979–1988	10	−59.8421	0.0305	0.0000	0.9318	0.0265	0.9630
		1989–2002	14	2.0678	−0.0007	0.4732	0.0437	0.0136	
Roundfish guild									
Inner	Richness	1979–2002	24	−5.0326	0.0040	0.8287	0.2175	0.6197	
Middle	Richness	1979–1986	8	865.6880	−0.4338	0.0119	0.6789	0.7895	0.9040
		1987–2002	16	203.6660	−0.1006	0.0000	0.7196	0.3095	
Outer	Richness	1979–1986	8	908.1290	−0.4564	0.0011	0.8511	0.5051	0.8690
		1987–2002	16	−65.9678	0.0340	0.0762	0.2075	0.3276	
Combined	Richness	1979–1986	8	1535.3000	−0.7713	0.0003	0.9072	0.6527	0.9410
		1987–2002	16	81.4226	−0.0394	0.1204	0.1634	0.4390	
Inner	Evenness	1979–1990	12	−14.9002	0.0078	0.3003	0.1066	0.0853	0.5620
		1991–2002	12	−32.0753	0.0164	0.0057	0.5504	0.0561	
Middle	Evenness	1979–1990	12	51.5981	−0.0257	0.0001	0.7779	0.0518	0.9210
		1991–2002	12	20.3337	−0.0099	0.0002	0.7694	0.0206	
Outer	Evenness	1979–1987	9	66.1545	−0.0331	0.0024	0.7550	0.0552	0.7150
		1988–2002	15	−16.5892	0.0085	0.0110	0.4028	0.0482	
Combined	Evenness	1979–1989	11	46.7485	−0.0233	0.0003	0.7782	0.0434	0.8630
		1990–2002	13	1.1549	−0.0003	0.8818	0.0021	0.0306	

armorhead sculpin (*Gymnocanthus galeatus*), snailfishes (*Liparis gibbus* and *Careproctus rastrinus*), marbled eelpout (*Lycodes raridens*), and wattled eelpout (*Lycodes palearis*), and in outer domain species such, as shortfin eelpout (*Lycodes brevipes*) and sablefish (*Anoplopoma fimbria*). There has been a increase in large sculpins, including the bigmouth sculpin (*Hemitripterus bolini*) and the great sculpin (*Myoxocephalus polyacanthocephalus*), in the outer domain. The biomass of skates predominantly the Alaska skate (*Bathyraja parmifera*), increased considerably from 1979 through 1990, followed by a prolonged period of little change from 1990 through 2002.

Flatfish biodiversity

Eleven species or species groups were used for biodiversity indexes for the flatfish guild (Table 1). All 11 species are rarely found together, and within each shelf domain the major portion of the assemblage comprises 3–5 species. Figure 3 shows the change in biodiversity indexes from 1975 to 2002 for each domain separately and all domains combined. The piecewise model shows a period of inflection for evenness and richness indexes for flatfish in the inner and middle domains that occurred between 1987 and 1993, with the average year of inflection being 1990 (Fig. 3, Table 3). The outer domain for flatfish showed little change in evenness and richness throughout the 24-year study period. Three species dominated the entire period, with somewhat evenly distributed biomass proportions.

Roundfish biodiversity

Forty-one species or species groups were used in the roundfish biodiversity analysis (Table 2). The evenness and species richness index for the roundfish group

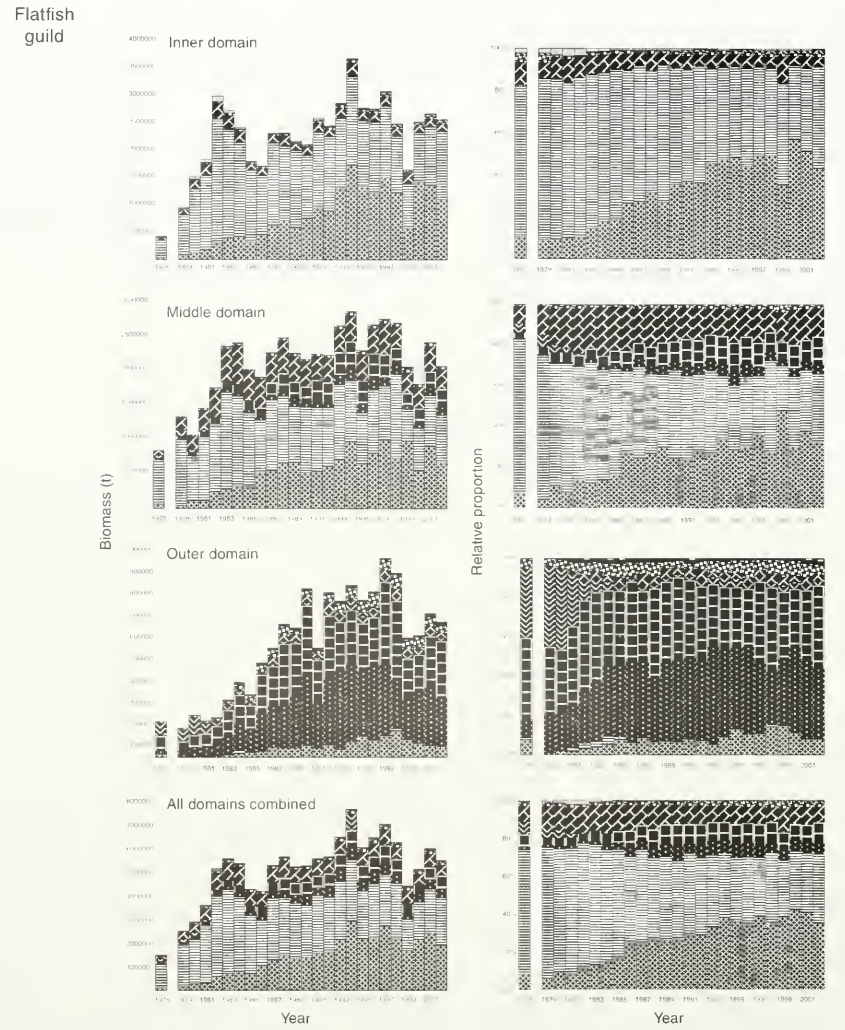
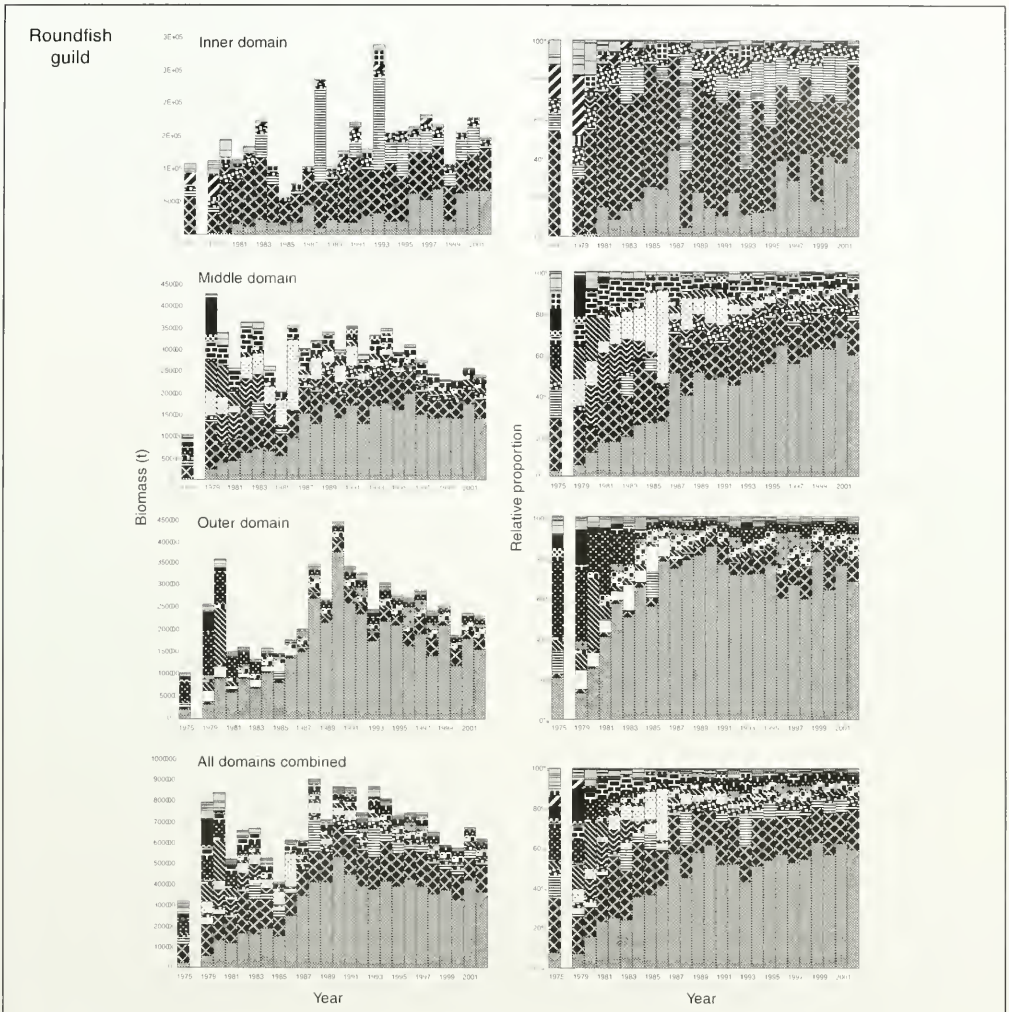


Figure 2

Biomass estimates for flatfish guild and roundfish guild (left panel), and relative proportion of each species (right panel) for inner, middle, outer, and all three domains combined, respectively.



Roundfish guild

- Atka mackeral
- prowfish
- pricklebacks
- salmon
- hagfish and lampreys
- sharks
- arctic cod
- Pacific tomcod
- rainbow smelt
- eulachon
- Pacific sand lace
- Pacific sandfish
- other sculpins
- *Icelus* sculpins
- spinyheaded sculpin
- *Triglops* sculpins
- darkfin sculpin
- armorhead sculpin
- Bering wolffish and wolfeel
- Bering poacher
- sawback poacher
- other poachers
- searcher
- lumpsuckers
- capelin
- saffron cod
- other eelpouts
- snailfishes
- white spotted greenling
- yellow Irish lord
- shortfin eelpout
- rockfish
- bigmouth sculpin
- wattled eelpout
- butterfly sculpin
- marbled eelpout
- sturgeon poacher
- sablefish
- Pacific herring
- *Myoxocephalus* sculpins
- skates

Figure 2 (continued)

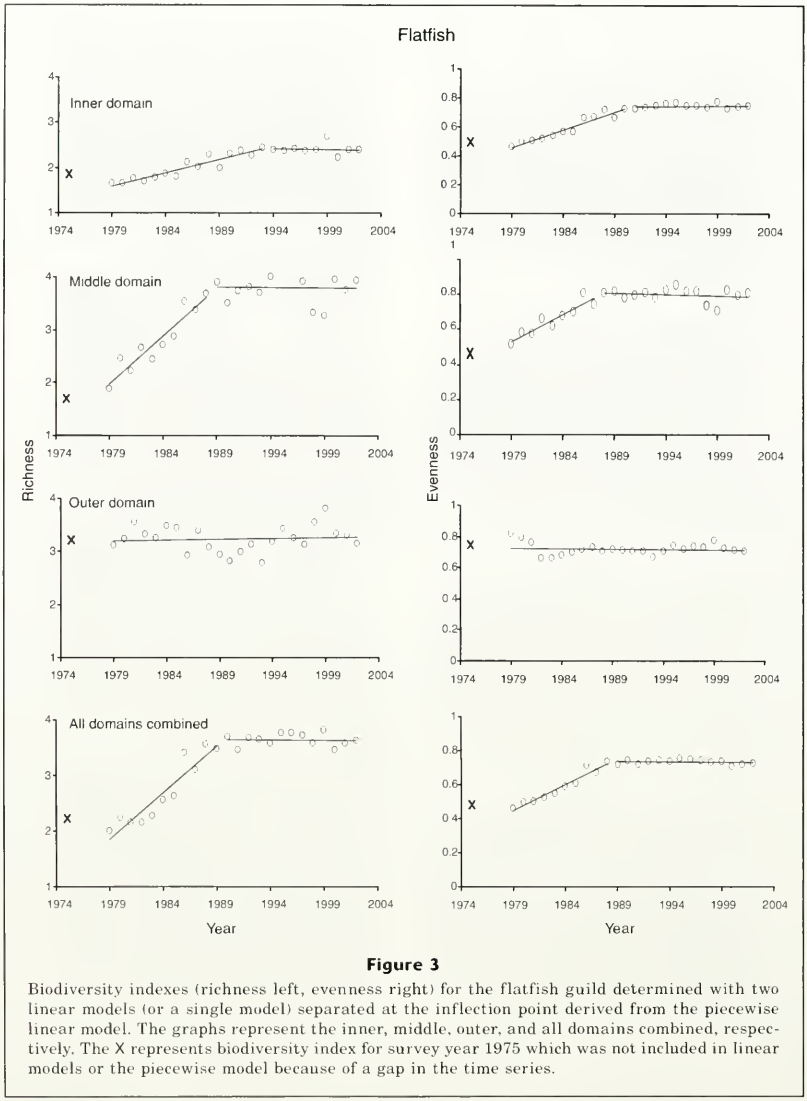


Figure 3

Biodiversity indexes (richness left, evenness right) for the flatfish guild determined with two linear models (or a single model) separated at the inflection point derived from the piecewise linear model. The graphs represent the inner, middle, outer, and all domains combined, respectively. The X represents biodiversity index for survey year 1975 which was not included in linear models or the piecewise model because of a gap in the time series.

is plotted for each shelf domain and for all domains combined. The inner domain richness index revealed a steady level of approximately 2–3 dominant species or species groups (*Myoxocephalus* sculpins, skates, and Pacific herring) over the 24-year period. The gradual increase in skates and slight decline in the plain sculpin caused an increase in the evenness index to somewhat even proportions of the three dominant species in the inner domain, from 7 to 2 dominant species over the 24-year period, and evenness declined by about one-half (Fig. 4). The increase in skates and decline of many inner domain species from 1975 through the early 1990s resulted in an assemblage dominated by two species groups, *Myoxocephalus* sculpins and skates (Fig. 2).

The outer domain showed a dramatic decline in richness and evenness from 1975 to the mid-1980s and

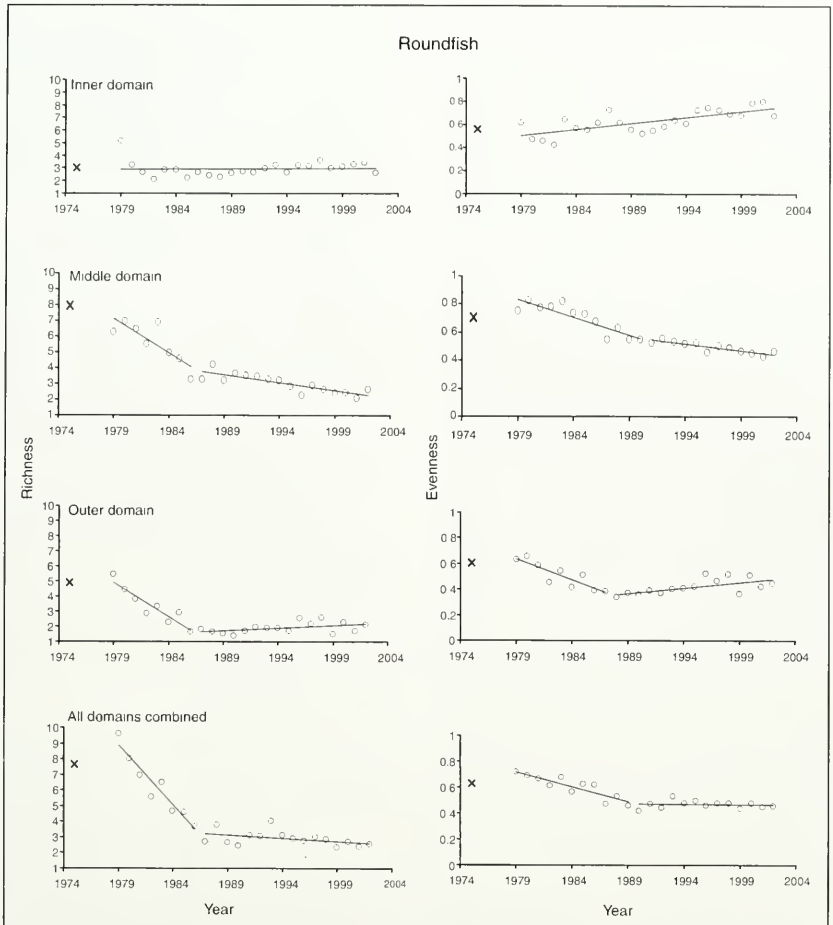


Figure 4

Biomass estimates of roundfish guild (left panel), and relative proportion of each species (right panel) for the inner, middle, outer, and all domains combined, respectively.

then a slight increase through 2002. A decrease in the number of dominant species, such as sablefish, wattled and shortfin eelpouts from 1979 to 1986, and a large increase of skate biomass from 20% in 1975 to approximately 75% of the total biomass by 1986, explain the index decline during this same period as the skate biomass dominated. After 1986 the skate populations stabilized somewhat to a slight decline which accounts for the slight increase in evenness and richness as other species gained a larger percentage of the total biomass.

All indexes for the roundfish guild, except for inner domain richness, indicated two distinct linear periods. Inflection points ranged from 1986 to 1990 and 1988 was an average inflection year for the roundfish guild.

Discussion

Periods of climatic change have been shown to instill long-term changes in the North Pacific ecosystem (Hare

and Mantua, 2000). Biodiversity indexes are a robust measure for large ecosystem monitoring and possible indicators of resulting regime shift phenomenon from climatic change based on an assemblage's long-term responses. Hare and Mantua (2000) summarized over 100 studies from the eastern North Pacific identifying two distinct periods of change or "regime shifts" in 1977 and 1989. Recently, Stabeno et al. (2001) and Hunt and Stabeno (2002) suggested the possibility of a third period of significant climatic change in the late 1990s for the northeastern Pacific. Although environmental changes may be readily identified, the ecosystem fauna may respond more slowly, or in ways not immediately obvious; however the changes may be persistent and far reaching. According to survey data, the last 20 years have proven to be a very hospitable environment for many flatfish species in the EBS, where populations such as northern rock sole and arrowtooth and Kamchatka flounder have rapidly expanded since the late 1970s. Biodiversity indexes are significantly higher than they were 20 years ago for flatfish as a group and have remained high and unchanged. The biodiversity indexes for flatfish guild corroborate the timing of the strong regime shift reported in the late 1980s. An inflection around 1990 is the strongest evidence of a regime shift from the biodiversity indexes. It would be expected that a purely biological response to a climatic event may lag by a time period, perhaps accounting for a later year than previously reported.

Survey data indicate that many roundfish species have not fared as well as flatfish species and biodiversity indexes are significantly lower now than 20 years ago. The roundfish guild has undergone a significant reorganization in which a large group of species have declined and a single species has become dominant, causing biodiversity to be suppressed. The regime shift is reflected in the roundfish biodiversity around 1988, which agrees with the results of other reported studies.

Although EBS productivity has increased through the 1970s and 1980s and remained high through the 1990s, the trend in the ecosystem is towards fewer or single dominant species. The decline of many nonexploited species in the EBS is difficult to explain with the current regime shift theories. Unfortunately, a lack of information on the life history of the large number of species, such as poachers, sculpins, eelpouts, and skates in the EBS hinders a complete understanding of recruitment success or failure.

Acknowledgments

I thank all the dedicated scientists, vessel skippers, and crew for their hard work over the years collecting data and G. Walters and M. Martin for assistance with data analysis. Also I thank the reviewers for their contributions in improving this manuscript. The reviewers were D. Somerton, G. Walters, J. Orr, S. Kotwicki, G. Stauffer, A. Hollowed, and an unknown journal reviewer. Thank you all.

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Abstract—A new species of the cottid genus *Triglops* Reinhardt is described on the basis of 21 specimens collected in Aniva Bay, southern Sakhalin Island, Russia, and off Kitami, on the northern coast of Hokkaido, Japan, at depths of 73–117 m. Of the ten species of *Triglops* now recognized, the new species, *Triglops dorothy*, is most similar to *T. pingeli* Reinhardt, well known from the North Atlantic and North Pacific oceans and throughout coastal waters of the Arctic. The new species differs from *T. pingeli* in a combination of morphometric and meristic characters that includes most importantly the number of dorsolateral scales; the number of oblique, scaled dermal folds below the lateral line; and the number of gill rakers.

Triglops dorothy, a new species of sculpin (Teleostei: Scorpaeniformes: Cottidae) from the southern Sea of Okhotsk

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Sculpins of the teleost family Cottidae are nearly ubiquitous in cold-water benthic habitats of the Northern Hemisphere, comprising nearly 200 species in the North Pacific alone (Yabe and Nakabo, 1984; Sheiko and Federov, 2000; Mecklenburg et al., 2002; Love et al., 2005), where they are found in almost every benthic habitat from the intertidal to the upper continental slope. Many species are preyed upon by larger fishes and marine mammals (Browne et al., 2002), and are themselves predators primarily of smaller fishes and crustaceans (e.g., Tokranov, 1998; Hoff, 2000; Tokranov and Orlov, 2001). Although many members of the family are also commonly found in bycatch of commercial fisheries (Stevenson, 2004; Orlov, 2005), the systematics and life histories of most species are poorly known (Nelson, 1994; Hoff, 2000; Hoff, 2006) and new species continue to be described (e.g., Yabe, 1995; Yabe and Maruyama, 2001; Yabe et al., 2001). A more complete understanding of the diversity of the family is necessary to understand the role of cottids in the dynamics of North Pacific ecosystems.

The cottid genus *Triglops* Reinhardt (1830), including *Prionistius* Bean (1884), *Elanura* Gilbert (1896), and *Sternias* Jordan and Evermann (1898) as junior synonyms, contains 19 nominal species and subspecies, of which nine are currently recognized as valid (Pietsch, 1993). Members of the genus are characterized most strikingly by having a small head, a narrow, elongate body and a slender caudal peduncle, a long anal fin containing 18–32 rays, pelvic fins with a single spine and three soft rays, branchiostegal membranes united on the ventral midline but lying free from the isthmus, and scales below the lateral line modified to form discrete rows of tiny serrated plates that lie in close-set, oblique dermal folds. The species are generally distributed in rather deep water (primarily between 18 and 600 m, but specimens have been taken more or less on the surface and as deep as 930 m; Andriashev, 1949; Hart, 1973; Fedorov, 1986) throughout cold-water, continental shelf or slope regions of the North Pacific, North Atlantic, and Arctic oceans. All appear to feed primarily on small planktonic and benthic invertebrates (Andriashev, 1949; Fedorov, 1986). Spawning takes place from late summer to winter; the eggs are demersal (Andriashev, 1949; Musick and Able, 1969; Fedorov, 1986).

Triglops was first proposed by Johannes Reinhardt (1830), based on a single specimen from West Greenland, but the type species *T. pingeli*

Manuscript submitted 28 March 2005 to the Scientific Editor.

Manuscript approved for publication 16 August by the Scientific Editor.

Fish. Bull. 104:238–246 (2006).

was not named until 1837, after Reinhardt received two additional specimens, also from West Greenland. During the next 130 years, 18 additional species or subspecies were described, but little work of a comparative nature was done. Schmidt (1930) reviewed some North Pacific specimens of the group, and later (Schmidt, 1950) discussed species identified in his work on the ichthyofauna of the Sea of Okhotsk. Taranets (1941) placed the genus, together with *Sternias*, in its own subfamily. The Arctic and North Pacific species of *Triglops* were studied by Jensen (1944), Andriashev (1949, 1954), and McAllister (1963), and a world-wide revision of the genus was subsequently published by Pietsch (1993).

Within the material of *Triglops* examined by Pietsch (1993) are 19 specimens that were originally recognized by Charles Henry Gilbert as new to science (see "Discussion" below). Labeled as such, but left unpublished by Gilbert, Pietsch (1993) came to the same conclusion, citing a lack of agreement of these specimens with the diagnosis of any of the nine recognized species of the genus. However, still not totally convinced that the specimens represented a new species, Pietsch (1993) again postponed a formal description. Labeled *Triglops* sp. and set aside at that time, these specimens are now re-examined in light of the discovery of two additional specimens, and evidence is provided to formally recognize the material as a new species.

Methods and materials

Standard length (SL) is used throughout unless indicated otherwise. Measurements are expressed in percent of standard length or in percent of head length (HL). Methods used for taking counts and measurements follow those described and figured by Miller and Lea (1972:7–12), with the following additions: interorbital width is measured between lateral margins of the frontal bones at their narrowest widths; head depth is measured at mid-orbit; first infraorbital pore width is measured at the greatest width, anterior to posterior; all gill-raker counts are taken from the first arch; dorsolateral scale-row counts include all scales (or fused clusters of scales) with enlarged plate-like bases; lateral-line scale counts also include scales that occasionally extend beyond the posterior margin of the hypural plate. Pectoral-fin rays are counted from dorsal to ventral. Counting the oblique dermal folds on the ventral half of the trunk presents a special problem. Because many dermal folds (the number depending on the species), which originate along the lateral line, terminate irregularly before reaching the ventral midline, counts can be considerably higher and more highly variable (than the values reported in the present study) if made along a transect close to the lateral line; thus, it is important to count the dermal folds along a transect beginning beneath the pectoral fin and continuing along, close to and strictly parallel with, the base of the anal fin (see Pietsch, 1993:337, Fig. 1). Dermal folds of the breast are counted along the ventral mid-line. Symbolic codes for institutions are those provided by Leviton et al. (1985).

Statistical significance was assessed by ANOVA; all differences at $P<0.05$ were considered significant. To aid in the discrimination of the new species and its closest ally, *T. pingeli*, a standard principal component analysis (PCA) was conducted on meristic characters, and a sheared PCA was conducted on morphometric characters for a size-free analysis. The analyses were conducted on the correlation matrix of raw meristic data and the covariance matrix of log-transformed raw morphometric data. Differences between species were illustrated by plotting principal component (PC) 1 against PC2 of the meristic analysis, sheared PC2 against sheared PC3 of the morphometric analysis, and sheared morphometric PC2 against the standard meristic PC1.

Following the PCA, a linear discriminant function analysis (DFA) was conducted on morphometric and meristic data to establish the relative significance of those characters in distinguishing the species. Morphometric data were standardized by dividing by standard length. Each character was tested to verify assumptions of multivariate normality and for statistical significance; those found to be distributed nonnormally or that were nonsignificant were eliminated from further analysis. The robustness of the DFA was tested by conducting a leave-one-out cross-validation procedure. Statistical analyses were performed with S-Plus (vers. 6.1 for Windows, 2002, Insightful, Inc., Seattle, WA) and SPSS (vers. 11.5.1 for Windows, 2002, SPSS Inc., Chicago, IL).

Systematics

Triglops dorothy Pietsch and Orr, n. sp.

Dorothy's sculpin

Figures 1–4, Tables 1–3

Triglops sp.: Pietsch, 1993:379 (probably an undescribed species, description postponed).

Holotype

USNM (U.S. National Museum of Natural History, Washington, D.C.) 74578, female, 155 mm, *Albatross* Station 5013, Aniva Bay, 46°17′N, 143°09′E, 3-m Agassiz trawl, 77 m, substrata unknown, 25 September 1906.

Paratypes

Twenty specimens, 15 males (72.5–148.0 mm), 5 females (68.5–143.0 mm). The following material was collected by the U. S. Fish Commission Steamer *Albatross* in or adjacent to Aniva Bay, Sakhalin Island, Russia, with a 3-m Agassiz trawl: CAS-SU 22305, 3 females (68.5–133.0 mm), station 5007, 46°03′N, 142°31′E, 77 m, green mud, fine gray sand, 24 September 1906. USNM 74575, 2 males (72.5–80.0 mm), station 5006, 46°04′N, 142°29′E, 79 m, green mud, fine gray sand, 24 September 1906;

Figure 1

Triglops dorothy n. sp., holotype, female, 155 mm, USNM 74578.

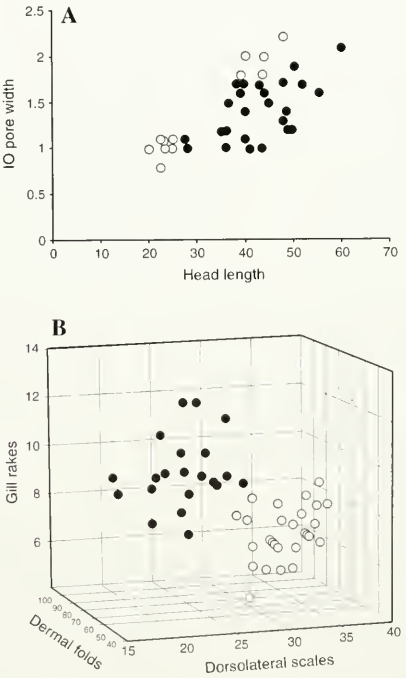

Figure 2

Plots of significant characters differentiating *Triglops dorothy* n. sp. (○) from *Triglops pingeli* (●) in the Sea of Okhotsk: (**A**) width of first infraorbital (IO) pore versus head length; (**B**) Counts of gill rakers versus dermal folds versus dorsolateral scales.

USNM 74576, 3 males (73.0–77.5 mm), 1 female (83.0 mm), station 5008, 46°07′50″N, 142°37′20″E, 73 m, green mud, fine gray sand, 24 September 1906; USNM 74577, female (143.0 mm), station 5016, 46°44′30″N, 143°45′E, 117 m, brown mud, fine black sand, rock, clay, 25 September 1906; USNM 74579, 8 males (73.5–80.0 mm), station 5005, 46°04′40″N, 142°27′30″E, 77 m, green mud, fine gray sand, 24 September 1906. The following material was collected from off Kitami, Hokkaido, Japan, September 1964: HUMZ 41524, 1 male (132.0 mm); HUMZ 41525, 1 male (148.0 mm).

Diagnosis

A species of *Triglops* distinguished from all other described members of the genus in having the following combination of character states: interorbital width 8.9–11.5% HL; caudal fin truncate to slightly rounded; dorsolateral scales well developed, 18–31; lateral-line scales 47–50; transverse dermal folds of breast 4–10; oblique dermal folds 67–99; dorsal-fin rays 23–25; pectoral-fin rays 17–19; gill rakers 7–12; first infraorbital pore length 3.6–5.0% HL; peritoneum everywhere unpigmented or at most with few, widely spaced melanophores.

Description

Body relatively compressed, tapering gradually posteriorly (Fig. 1); head compressed, length 28.4–32.3% SL (Table 1), depth 11.3–13.5% SL; snout pointed, upper profile linear to slightly convex, length 27.4–36.3% HL, about equal to length of orbit; length of orbit 29.0–32.0% HL; upper jaw extending anteriorly slightly beyond lower; first infraorbital pore large, length 3.6–5.0% HL (Fig. 2A); gill rakers 7–12 (Table 2), 0–1 on upper part of arch, 6–11 on lower part of arch, short and blunt; longest pectoral-fin ray 20.9–25.0% SL (sexually dimorphic; see below); third pelvic-fin ray 12.6–17.7% SL, longer than first and second; length of pelvic fin sexually dimorphic (see below); caudal peduncle compressed or roughly circular in cross section, length 14.7–18.3% SL, depth 3.1–4.1% SL. Skin covering elements of upper and lower

Table 1

Proportional morphometrics and meristics of *Triglops dorothy* n. sp. and of *T. pingeli* from the Sea of Okhotsk. Morphometric data are presented in percent of standard length (in mm). Statistical significance was tested by ANOVA when appropriate; ns = not significant.

	Triglops dorothy				*Triglops pingeli*			
	Holotype	*n*	Range	Mean ±SD	*n*	Range	Mean ±SD	Significance
Measurements								
Standard length (in mm)	155.0	21	68.5–155		27	88–184		
Snout length	9.0	20	7.9–9.6	8.9 ±0.5	27	6.8–10.1	9.1 ±0.7	
Orbit length	9.0	21	8.4–9.9	9.2 ±0.4	27	7.2–10.2	8.8 ±0.8	ns
Infraorbital pore width	2.2	12	0.7–2.3	1.3 ±0.4	27	0.5–1.9	1.1 ±0.4	$P<0.01$
Head length	31.0	21	28.4–32.3	29.9 ±0.9	27	26.4–33.6	30.5 ±1.6	
Head depth	12.3	19	11.3–13.5	12.5 ±0.5	27	11.0–14.5	12.5 ±0.8	
Interorbital width	3.0	21	2.7–3.5	3.1 ±0.2	27	2.1–3.4	2.7 ±0.4	$P=0.05$
Pectoral-fin ray length	22.6	21	20.9–25.0	22.8 ±1.2	27	20.5–29.6	23.8 ±2.4	ns
Pelvic-fin ray length	13.6	20	12.6–17.7	15.0 ±1.4	27	11.0–16.0	13.0 ±1.6	ns
Caudal-peduncle depth	3.7	21	3.1–4.1	3.7 ±0.2	27	2.6–4.3	3.5 ±0.3	ns
Caudal-peduncle length	15.5	21	14.7–18.3	16.8 ±1.0	27	14.7–21.1	16.8 ±1.7	ns
Counts								
Dorsolateral scales	31	21	18–31	25.0 ±3.3	27	28–37	32.9 ±2.9	$P<0.001$
Dermal folds	99	21	67–99	81.6 ±8.2	27	50–87	64.6 ±11.3	$P<0.001$
Breast scale rows	10	21	4–10	7.2 ±1.6	27	4–11	7.8 ±1.8	ns
Lateral-line scales	48	21	47–50	48.2 ±0.8	27	47–50	48.8 ±0.9	$P=0.02$
Dorsal-fin spines	11	21	10–11	10.9 ±0.3	27	10–11	10.7 ±0.4	
Dorsal-fin rays	24	21	23–25	24.1 ±0.6	27	23–27	25.0 ±0.9	ns
Anal-fin rays	24	21	23–25	23.8 ±0.5	27	22–25	23.7 ±0.7	ns
Pectoral-fin rays	18	21	17–19	18.1 ±0.5	27	18–21	19.3 ±0.8	$P<0.001$
Gill rakers	11	21	7–12	9.3 ±1.3	27	5–9	7.1 ±0.9	$P<0.001$
Vertebrae	12+34	21	11–12+33–35		4	12–13+32–36		

Table 2

Counts of dorsolateral scales, dermal folds, and gill rakers on the first arch of *Triglops dorothy* n. sp. and *Triglops pingeli* from the Sea of Okhotsk.

Dorsolateral scales

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
T. dorothy	1	1		1	1	2	3	2	2	5		1	1							
T. pingeli											3	1	1	5	3	2		6	4	2

Dermal folds

	50	51	52	53	54	55	57	58	59	60	61	62	64	66	67	68	69	70	71	72	73	74	75	76	77	82	83	84	85	86	87	88	89	90	91	99
T. dorothy															1					2	1	2		1	2	1	2	1		2			1	1	1	2	1
T. pingeli	1	2	1	1	1	2	1	2			1	1	2	3	1				1			1	1		1		2		1							

Gill rakers

	5	6	7	8	9	10	11	12
T. dorothy			2	1	12	2	2	2
T. pingeli	1	5	13	7	1			

jaws, throat, ventral portion of cheeks, interopercle, extreme ventral tip of subopercle, and extreme dorsal margin of gill membrane naked; remaining part of head and dorsal half of body everywhere covered with rough, granular scales; approximately 10–16 close-set rows of tiny granular scales on anterior and dorsal periphery of eyeball, rows usually extending nearly to dorsalmost margin of eye. Oblique dermal folds terminating on caudal peduncle well before reaching ventral midline but sometimes crossing space between anus and base of anal fin. Dorsal-fin spines 10–11, anal-fin rays 23–25; vertebrae 45–47.

Color in preservation: dark brown dorsally, light brown, tan, to cream ventrally, with four dark saddles along dorsal length of body extending ventrally to, and sometimes slightly below, lateral line, anteriormost saddle situated beneath spinous dorsal fin, two beneath soft dorsal fin, posteriormost saddle on caudal peduncle; most specimens with a small saddle or narrow band of pigment crossing soft-dorsal fin at midlength (homologous to fifth saddle of many congeners). A series of dark, more-or-less equally spaced spots or streaks extending along length of body just ventral to lateral line, spots nearly always interconnected in males to form a conspicuous dark stripe across length of body, but not extending onto caudal-fin base. Anterior portion of lower lip darkly pigmented, sometimes interrupted at symphysis of jaw; upper lip with a dark streak across symphysis and two or three similar, more-or-less equally spaced streaks on each side, posteriormost streak contiguous with similar spot or streak on maxilla (pigmentation of lips more intense in males); males with a streak of pigment extending along dorsal margin of upper jaw from ventral margin of lacrimal to beneath and slightly past eye; a large, diffuse spot posterior to distal tip of maxilla (more heavily pigmented in males), sometimes forming an oblique streak extending from posterodorsal margin of maxilla posteroventrally to preopercle. Dorsomedial surface of opercle and posterodorsal margin of gill membrane densely covered with small melanophores, pigment extending ventrally along medial surface of branchiostegal rays (pigmentation often bleached away in old, poorly preserved material); lateral surface of distal portion of four or five posteriormost branchiostegal rays, as well as gill membrane in between, heavily peppered with small melanophores. Each spine and ray of dorsal fin (but not membrane in between) with two to four, dark, more-or-less equally spaced spots. Four to seven narrow, more-or-less equally spaced bands of dark pigment across dorsalmost or nonexerted rays of pectoral fin; a small, dark spot at dorsal insertion of pectoral fin often continuous with pigment extending ventrally to mid-base of fin. Anal fin usually unpigmented, but some specimens with rays darkly pigmented or lined with rows of melanophores, pigmentation especially intense in males; pelvic fins usually unpigmented, but some males with distal tips of first and second rays lightly pigmented. Base of caudal fin with dark dorsal and ventral spots, ventral spot usually more distinct than dorsal; males with a dark spot near distal end of dorsal and ventral lobes of caudal fin, sometimes faint and difficult to discern in preserved specimens.

Sexual dimorphism

Females with pectoral-fin rays slightly shorter (22.6–23.4% SL) than those of males (20.9–25.0% SL). Females with pelvic-fin rays slightly shorter (12.6–14.7% SL) than those of males (12.7–17.7% SL); tissue surrounding pelvic-fin spine and first ray expanded in males.

Statistical analyses

Univariate analyses of morphometric characters indicated that only interorbital width and the length of the first infraorbital pore exhibited significant differences between *T. dorothy* and *T. pingeli* (Table 1). The analyses of meristic characters, on the other hand, revealed significant differences in several characters, including fewer dorsolateral scales, lateral-line scales, and pectoral-fin rays, and a greater number of dermal folds and gill rakers in *T. dorothy* than in *T. pingeli* (Table 1). Three-way plots of dorsolateral scales, dermal folds, gill rakers, and pectoral-fin rays exhibit a clear separation between *T. pingeli* and *T. dorothy* (Fig. 2B).

In plots of scores from the PCA of meristic characters, two distinct clusters, one for each of the two species, were evident (Fig. 3A). The primary axis of separation was PC1 (30.2% of total variance), which was heavily loaded positively on dorsolateral scales and gill rakers and negatively on lateral-line scales; loadings along the PC2 axis (22.4% of total variance) were heavily loaded positively for breast-scale rows and negatively for anal-fin rays and dorsal-fin rays (Table 3). In contrast, broad overlap was displayed in the analysis of morphometric characters, with individuals of *T. dorothy* clustering among the larger group of *T. pingeli* from the Sea of Okhotsk (Fig. 3B). The first principle component (PC) was interpreted as a size component accounting for 95.5% of the total variance. In plots of the scores of the sheared second and third shape components (1.5% and 1.1% of total variance, respectively), the greatest dispersion was along the PC2 axis (Fig. 3B, C), and loadings along this axis were highest for interorbital width, snout length, and caudal-peduncle depth (Table 3). Loadings along the PC3 axis were highest for pectoral-fin ray length, ventral caudal-peduncle length, and orbit length (Table 3).

The single linear discriminant function equation produced was highly significant (χ^2=96.5, 6 df, P<0.0001):

$$D = 0.894(ds) - 0.691(g) + 0.530(p) - 0.508(df) - 0.284(io) + 0.098(ll),$$

where D = the discriminant score of an individual;
ds = number of dorsolateral scales;
g = number of gill rakers;

Table 3

Factor loadings for standard principal component (PC) analysis of meristic characters and sheared PC analysis of morphometric characters for *Triglops dorothy* n. sp. and for *T. pingeli* from the Sea of Okhotsk.

	PC1	PC2	PC3
Meristics			
Dorsal-fin rays	−0.3678	−0.4269	0.1352
Lateral-line scales	−0.3886	−0.1695	0.2437
Anal-fin rays	−0.2007	−0.5078	0.3611
Dermal folds	−0.4517	−0.0691	0.4440
Pectoral-fin rays	−0.3750	0.3030	0.3137
Dorsolateral scales	−0.3668	0.3919	0.2438
Breast scale rows	0.0861	0.4464	0.4980
Dorsal-fin spines	0.1918	0.1278	0.0765
Gill rakers	0.3875	−0.2560	0.4281
Morphometrics			
Standard length	0.3446	0.0348	0.0764
Snout length	0.3541	0.2603	−0.2662
Orbit length	0.3117	0.2043	−0.4521
Head length	0.3547	0.15793	−0.1867
Head depth	0.3340	0.0861	−0.2887
Interorbital width	0.2999	−0.7286	−0.0446
Pectoral-fin ray length	0.3431	0.2007	0.5844
Caudal-peduncle depth	0.3266	−0.5013	0.0598
Caudal-peduncle length	0.3271	0.1857	0.5036

p = number of pectoral-fin rays;
df = number of dermal folds;
io = interorbital width divided by SL; and
ll = number of lateral-line scales.

All individuals with negative scores had been previously identified as *T. dorothy*, whereas those with positive scores were *T. pingeli*. The discriminant function equation correctly classified all individuals, as did the cross-validation procedure.

Distribution and habitat

Triglops dorothy is known only from the southern Sea of Okhotsk: 19 specimens collected in or adjacent to Aniva Bay, at the southern end of Sakhalin Island, Russia; and two specimens from north of Kitami, Hokkaido (Fig. 4). The material was trawled off bottoms of mud, fine sand, rock, and clay, at depths of 73–117 m.

Etymology

The species is named in honor of Dorothy Thomlinson Gilbert, great granddaughter-in-law of the eminent ichthyologist and fisheries biologist Charles Henry Gilbert, for her generous and steadfast support to graduate students in ichthyology at the University of Washington, Seattle, in establishing the William W. and Dorothy T. Gilbert Ichthyology Research Fund. The specific epithet is to be treated as a noun in apposition.

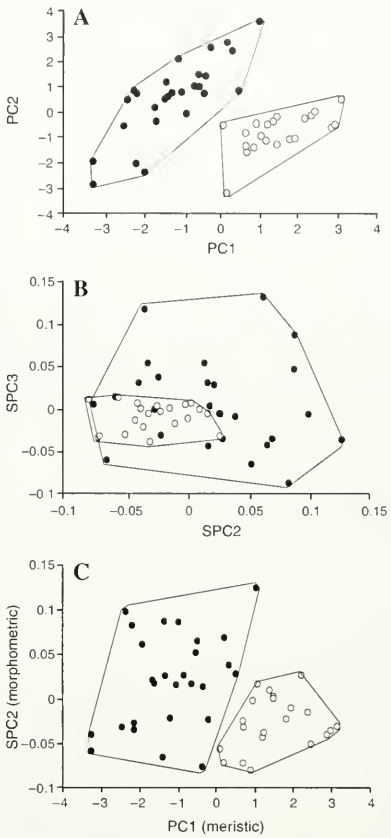

Figure 3

Plots of sheared principal component (SPC) and standard principal component (PC) scores for morphometric and meristic characters of *Triglops dorothy* n. sp. (•) and *T. pingeli* (○): (**A**) meristic characters only; (**B**) morphometric (SPC2 and SPC3) characters only; (**C**) morphometric (SPC2) and meristic characters (PC1).

Discussion

Credit for the discovery of *T. dorothy* is given to Charles Henry Gilbert (Pietsch, 1993; for biographical information on Gilbert, see Dunn, 1997), who, soon after the material was collected, recognized its uniqueness.

Although the USNM catalog ledger has "cotype" handwritten next to each catalog number (all 19 CAS-SU and USNM specimens are labeled as such) and Smithsonian Institution accession file no. 54484, dated 6 September 1912, lists the material as "co-types described by Dr. Gilbert" (Palmer[1]), a description was never published.

Why Gilbert, on closer inspection, chose not to formally recognize *T. dorothy* is probably because of its extreme similarity to *T. pingeli*. *Triglops dorothy* is easily confused with the latter species, but can be distinguished satisfactorily on the basis of only three meristic characters that overlap slightly between the two species in the Sea of Okhotsk (Tables 1–2): the number of oblique, scaled dermal folds below the lateral line (67–99 in *T. dorothy* versus 50–87 in *T. pingeli*), the number of dorsolateral scales (18–31 in *T. dorothy* versus 28–37 in *T. pingeli*), and the number of gill rakers (7–12 in *T. dorothy* versus 5–9 in *T. pingeli*). A significant difference in the length of the first infraorbital pore (Fig. 2A) reflects differences in the overall shape of the snout of the two species. In *T. dorothy*, the snout is slightly shorter and slightly more ventrally oriented than in *T. pingeli*.

Triglops dorothy is known only from the shallow continental shelf of the southern Sea of Okhotsk between Sakhalin Island and Hokkaido, an area that is thought to have served as a refugia for other species during the Quaternary glacial maximum (see Noll et al., 2001; Brykov et al., 2003). During this period, glaciers extended to just north of Terpeniya Bay on Sakhalin Island and to central Iturup Island in the southern Kurils, leaving the southern and central part of the Sea of Okhotsk ice-free. This region is thought to have been relatively isolated during this time from the Pacific Ocean and the Sea of Japan because of lower sea levels that connected the southern coastlines from Sakhalin to Hokkaido and the southern Kuril Islands (Kryvolutskaya, 1973; Pietsch et al., 2001; 2003). These land connections may have served to split and isolate populations of benthic marine fishes, such as *T. pingeli*, providing the opportunity for allopatric speciation of *T. dorothy*.

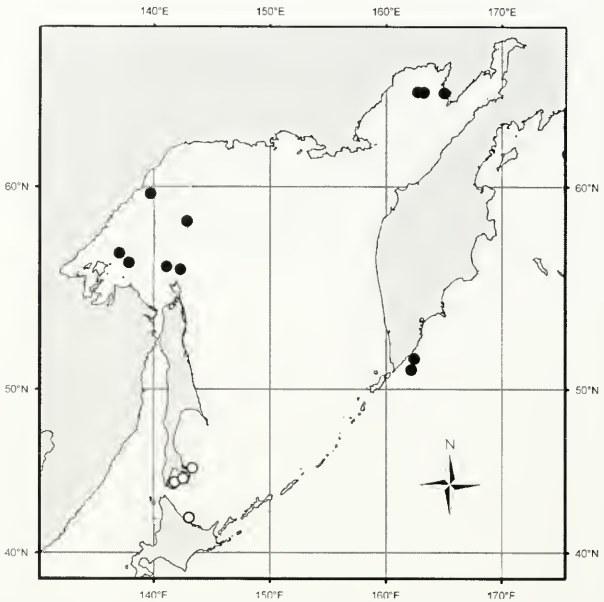

Figure 4

Distribution of *Triglops dorothy* n. sp. (○) and *T. pingeli* (•) in the Sea of Okhotsk based on material examined. Each symbol may represent more than one capture.

Acknowledgments

We thank the many people who made material available, especially W. N. Eschmeyer, T. Iwamoto, and D. Catania (CAS); S. L. Jewett, L. F. Palmer, and J. T. Williams (USNM); and M. Yabe (HUMZ). K. P. Maslenikov (UW) provided curatorial assistance. We are grateful also to two anonymous reviewers who greatly improved the final draft of the paper. A presubmission draft was critically read by J. R. Dunn (UW) and D. E. Stevenson (Alaska Fisheries Science Center, Seattle). The work was supported by the National Science Foundation under contract number DPP74-13988 to the Smithsonian Institution, F. D. Ferrari, principal investigator.

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Appendix—Comparative material examined

Triglops pingeli: HUMZ 54593 (female, 164 mm), HUMZ 54594 (female, 180 mm), HUMZ 54674 (male, 158 mm), HUMZ 55266 (female, 184 mm), HUMZ 55267 (female, 165 mm), HUMZ 55268 (female, 176 mm), West Kamchatka, 59°00′N, 168°00′E, 80 m, 5 June 1976; HUMZ 55052 (female, 170 mm), HUMZ 55055 (female, 171 mm), HUMZ 55058 (female, 167 mm), HUMZ 55062 (male, 154 mm), HUMZ 55089 (male, 150 mm), East Kamchatka, 51°25′N, 158°04′E, 135–140 m, 21 May 1976; HUMZ 55154 (female, 140 mm), Penjinskii Bay, 59°59′N, 160°00′E, 112–113 m, 6 June 1976; HUMZ 56400 (female, 104 mm), East Kamchatka, 50°58′N, 157°52′E, 242–245 m, 22 May 1976; HUMZ 56466 (female, 127 mm), Gizhiga, 61°01′N, 158°17′E, 94–95 m, 7 June 1976; HUMZ 57984 (female, 120 mm), Sea of Okhotsk, 56°40′N, 143°22′E, 310 m, 22 September 1976; HUMZ 58051 (male, 114 mm), HUMZ 60855 (female, 119 mm), Sea of Okhotsk, 55°30′N, 139°00′E, 117 m, 7 September 1976; HUMZ 60702 (male, 123 mm), Sea of Okhotsk, 57°38′N, 141°00′E, 121 m, 14 October 1976; HUMZ 60799 (female, 121 mm), Sea of Okhotsk, 57°38′N, 141°00′E, 121 m, 14 October 1976; HUMZ 60808 (female, 140 mm), HUMZ 60810 (female, 126 mm), HUMZ 60811 (female, 124 mm), Sea of Okhotsk, 54°54′N, 142°57′E, 110 m, 6 September 1976; HUMZ 60919 (female, 88 mm), Gizhiga, 61°00′N, 158°41′E, 88–90 m, 7 June 1976; HUMZ 60941 (female, 125 mm), HUMZ 60952 (female, 125 mm), Sea of Okhotsk, 55°00′N, 142°02′E, 121 m, 6 September 1976; HUMZ 61063 (male, 120 mm), HUMZ 61068 (female, 128 mm), Sea of Okhotsk, 55°09′N, 139°38′E, 124 m, 7 September 1976.

A comparison of two fishery-independent survey programs used to define the population structure of American lobster (*Homarus americanus*) in the Gulf of Maine

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Abstract—The population structure and abundance of the American lobster (*Homarus americanus*) stock in the Gulf of Maine are defined by data derived from a fishery-independent trawl survey program conducted by the National Marine Fisheries Service (NMFS). Few sampling stations in the survey area are located inshore, in particular along coastal Maine. According to statistics, however, more than two thirds of the lobster landings come from inshore waters within three miles off the coast of Maine. In order to include an inshore survey program, complementary to the NMFS survey, the Maine Department of Marine Resources (DMR) initialized an inshore survey program in 2000. The survey was modeled on the NMFS survey program, making these two survey programs comparable. Using data from both survey programs, we evaluated the population structure of the American lobster in the Gulf of Maine. Our findings indicate that lobsters in the Gulf of Maine tend to have a size-dependent inshore-offshore distribution; smaller lobsters are more likely to stay inshore and larger lobsters are more likely to stay offshore. The DMR inshore and NMFS survey programs focused on different areas in the Gulf of Maine and likely targeted different segments of the stock. We suggest that data from both survey programs be used to assess the lobster stock and to describe the dynamics of the stock in the Gulf of Maine.

Manuscript submitted 6 August 2004 to the Scientific Editor's Office.
Manuscript approved for publication 22 August 2005 by the Scientific Editor.
Fish. Bull. 104:247–255 (2006).

Many fish species experience size-dependent inshore-offshore movement at a certain stage (or stages) of their lives, resulting in size-dependent distribution. Shallow inshore waters along coasts in many parts of the world are primary nursery or spawning grounds (or both) for many commercially and recreationally important fish species (Taylor, 1953; Caddy, 1975). Juveniles of many fish species inhabit shallow inshore waters but migrate to deeper waters with increasing size (Chen et al., 1997). This size-dependent movement can also be observed in other life history stages such as when mature fish migrate to spawning grounds (Rowling, 1994). One consequence of such a size-dependent movement is that spatial distribution of fish becomes size-specific. Many ocean fish aggregate in their habitats according to size (Paloheimo and Dickie, 1964; Caddy, 1975; Hilborn and Walters, 1992).

The American lobster (*Homarus americanus*) is distributed throughout the northwest Atlantic from the Straight of Belle Isle, Newfoundland, to Cape Hatteras, North Carolina. It supports the most valuable commercial fishery in the Northeast United States (ASMFC, 2000). This lobster is most abundant in shallow coastal waters but can also be found in water depths of 700 meters (Cooper and Uzmann, 1980; Lawton and Lavalli, 1995). Various surveys and studies have indicated that there are large differences in lobster density among different areas and different water depths (Wahle and Steneck, 1992; Wilson, 1998; Palma et al., 1999).

Lobsters tend to move little during their first year on the bottom (Wahle, 1992; Palma et al., 1999). The daily and annual movement range increases with their sizes. After they reach harvestable size, their annual range of movement is about 2 to 3 kilometers (Krouse, 1980). Sublegal-size lobsters generally have small seasonal movements (<1 km/year) and are largely found near shore. Larger lobsters are more mobile (<20 km/year) and show progressively offshore deep

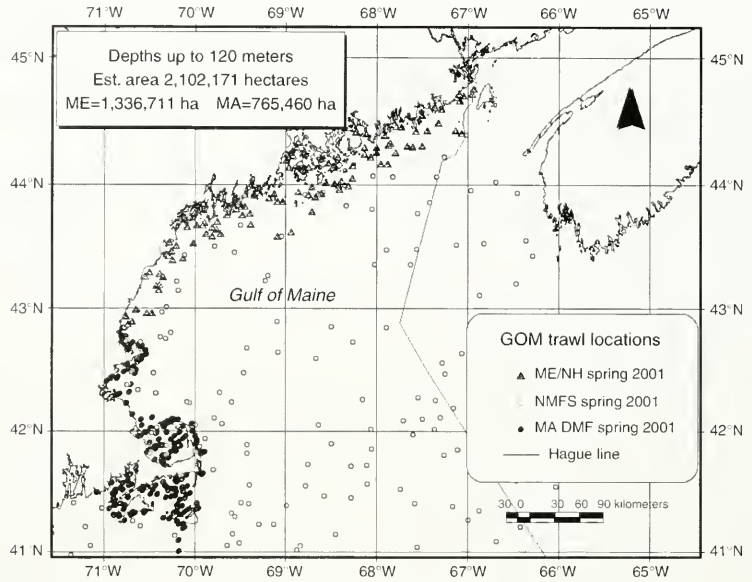

Figure 1

Geographical areas of the Maine Department of Marine Resources (DMF) inshore survey program and National Marine Fisheries Services NMFS survey program. ME/NH=Maine and New Hampshire; MA DMF=Massachusetts Department of Marine Fisheries.

movements in the fall, returning to inshore shallow areas in the spring.

The range of movement increases further after they reach maturity. However, there are large differences in migratory behaviors among individuals (Pezzack and Duggan, 1986). In general, mature legal-size lobsters are more abundant offshore and in deeper waters (Harding and Trites, 1989). Large egg-bearing lobsters have been shown to exhibit long migrations (>100 km) (Krouse, 1980; Campbell, 1983).

Size-dependent inshore-offshore distributions have been reported in many lobster studies (Skud, 1969; Cooper et al., 1975; Briggs, 1985; Campbell and Pezzack, 1986; Cobb et al., 1989; Harding and Trites, 1989). Information collected in commercial fisheries and scientific surveys has revealed that the spatial distribution of the American lobster may be size-dependent and that lobster of large sizes are more likely found in deep waters. This pattern has been identified but not quantified (Wilson, 1998). The spatial distribution of lobsters varies with seasons and scales with the size of lobsters.

The distribution and abundance of lobsters have been studied with a variety of techniques. Diver and submarine and ROV surveys are generally limited to nearshore areas or in temporal resolution. Tagging programs are often limited in area and time covered and in number of lobsters tagged and returned. A fisheries-dependent sea sampling program covers a limited number of fishing boats within limited areas and thus may not be able to provide an overall picture of lobster distribution and abundance within the lobster stock area in the Gulf of Maine. Until recently, the only comprehensive fishery-independent data were those obtained from the NMFS Gulf of Maine fall and spring trawl surveys. NMFS has conducted a randomized stratified survey since the mid 1960s, but this survey is limited to depths deeper than 50 meters. In fact, the majority of the sampling stations are located in waters deeper than 120 meters as a result of an increased proportion of untrawlable areas and problems with lobster gear in inshore waters. In the fall of 2000, the DMR began a coast-wide inshore trawl survey, which mainly covered waters shallower than 120 meters (Fig. 1).

The spatial distribution of lobsters is largely restricted to the nearshore areas. Although found throughout the Gulf of Maine, 80% of the landings are estimated to come within three miles from shore (ASMFC, 2000). Clearly the lobster fishery will follow the concentrations of lobsters, although seasonal changes in movements and trapability of lobsters may make less productive fishing areas desirable to limited portions of the fleet at certain times of the year. As the fishing effort for lobster has increased, the traditional inshore fishery

has expanded to nearshore waters (from 4.8 km to 32.2 km from shore). There is also a deepwater fishery for lobster that occurs farther from shore.

An optimal and effective fisheries management plan requires a high-quality stock assessment, which, in turn, is dependent on data collected from fisheries-dependent and fisheries-independent survey programs. One of the most important pieces of information used in a lobster stock assessment is the abundance index which is derived from the fisheries-independent bottom trawl surveys conducted by NMFS. Because trawling is difficult in coastal waters, few sampling stations in the NMFS survey are located inshore, specifically along coastal Maine from which the majority of the lobster landings are landed. Previous studies have also indicated that inshore habitats are critical to the lobster fishery. Thus, it is critical to develop an inshore survey program that can cover the waters off coastal Maine. The data collected from such a program can overcome the problem of a lack of inshore coverage in the NMFS survey. An inshore survey and the NMFS survey can complement each other for a more complete abundance index of the lobster stock in the Gulf of Maine.

In order to identify the importance of the DMR inshore survey, we compared the differences between the NMFS survey and DMR inshore survey in 1) the size composition of survey catches and their temporal trends; 2) temporal trends in abundance indices; and 3) average size and weight of lobsters. From our comparative study, we determined whether the lobster stock in the Gulf of Maine has a size-dependent inshore-offshore distribution and whether it is essential to include both sampling programs in a stock assessment to adequately describe the population dynamics of lobsters in the Gulf of Maine.

Methods and materials

Like the NMFS surveys, the inshore trawl survey is conducted during the spring and fall of each year. It has a stratified random design modeled after the NMFS and Massachusetts Department of Marine Fisheries (MADMF) surveys. The design has four depth strata (9–37 m, 37–64 m, 64–100 m, >100 m [its outer boundary roughly delineated by the 12-mile or 22-km limit]) and five regions based on oceanographic, geologic, and biological features. The fourth stratum was added in the spring of 2003. It expands the coverage area to equal the area in federal waters covered by the Atlantic States Marine Fisheries Commission (ASMFC) and allows some overlaps between annual inshore trawl survey area and the NMFS survey area. It also slightly reduces the sampling pressure in the shallower strata, which has been of concern to fixed-gear fishermen in the past. To randomize the survey area (~13,720 km^2), each depth stratum is divided into 1-nmi (i.e., 1.852 km) sampling grids. A target of 100 stations is selected for sampling in each survey, resulting in a sampling density of about 1 station /137 km^2. This density compares to the sampling density of the NMFS survey (1 station/892 km^2) and Massachusetts' survey (1 station/65 km^2). The number of stations per stratum is allocated in proportion to the area of each stratum. When a station is encountered that cannot be towed, an alternate tow is selected nearby over similar depth.

Trawl design considerations for the survey included effectiveness of the gear for sampling the complex bottom in the Gulf of Maine and approximate comparability with previous and ongoing surveys, such as that performed by the NMFS. Net tapers are cut to permit the shape of the net to be of maximum height, while allowing the net to remain tight on the bottom. The net is shackled from the footrope to the frame by using two 0.95-cm shackles on a banded wire that runs parallel with the footrope. Heavy rubber wing bobbins retard bottom wing lift. The top leg is constructed of 5.1-cm mesh overall and has a 1.3-cm mesh liner in the codend. Doors are 7.5 Bison doors. Attached to the 21.3-m-long, 1.59-wide footrope is a roller frame. The 3.05-m-wide bosom section is made up of 20.3-cm rubber disks on 15.2-cm centers, and there are eight evenly spaced toggles. The spacing is maintained by small 10.2-cm cookies strung between the disks. Chain sweeps were not used. The headrope is 17.4 meter in length.

Environmental data, including temperature and salinity profiles, wind, sea state, and weather, were collected at each station. A standard trawl tow, 20 minutes in duration, was made at each station. Shorter tow times were accepted under certain circumstances, such as the presence of fixed gears or untrawlable bottom in the survey pathway. Tow speed was maintained at 2.1 to 2.3 knots (i.e., 3.9 km/h to 4.3 km/h) and tow direction was oriented toward the tidal current whenever possible. All sampling was conducted during the day. After each tow, the net was brought aboard and emptied onto a sorting table. All individuals were identified and sorted by species. All lobsters were immediately separated and processed while the rest of the catch was sorted. Total weights (by sex), carapace length (mm), shell condition, presence and stage of eggs, V-notch condition, and injuries to the lobsters caused by the trawl were recorded. All lobsters were measured and the data were recorded in electronic format for analysis and made available on compact disk (CD). The data were geo-referenced and incorporated into geographic information systems (GIS) for analysis.

A no. 36 Yankee bottom trawl has generally been used in NMFS bottom trawl surveys. The trawl net is towed at approximately 3.5 knots (i.e., 6.5 km/h) for 30 minutes at each station. The survey is based on a stratified random design. Strata are defined according to water depth, latitude, and historical fishing patterns. Within each stratum, stations are assigned randomly; the number of stations allotted to a stratum is in proportion to its area (approximately one station per 892 km^2). Specifications for NEFSC standard no. 36 Yankee bottom trawl are defined by the NMFS.[1]

[1] NMFS (National Marine Fisheries Service). Website: http://www.nefsc.noaa.gov/femad/ecosurvey/mainpage. [Accessed August 2004.]

The trawl used in the DMR survey is similar in design, but smaller than that used in NMFS, although the size of the mesh liner in the codend is the same. The DMR survey trawl net is also towed for less time (20 minutes versus 30 minutes for NMFS).

The data collected in the inshore survey were analyzed according to the methods described below. The stratified mean number of lobsters per tow, $\bar{X}$, can be calculated as

$$\bar{X} = \frac{1}{A}\sum_{k=1}^{g} A_k \bar{X}_k,$$

where g = the number of stratum in the survey;
A_k = the survey area in stratum k;
A = the total area covered by the survey ($A=\sum_{k=1}^{g} A_k$); and
$\bar{X}_k$ = the average catch per tow in stratum k.

The $\bar{X}_k$ can be calculated as

$$\bar{X}_k = \frac{1}{T_k}\sum_{t=1}^{T_k} X_{k,t},$$

where $X_{k,t}$ = catch in tow t, stratum k; and
T_k = the total number of tow in stratum K.

The variance for the stratified mean, $S^2(\bar{X})$, can be estimated as

$$S^2(\bar{X}) = \frac{1}{A^2}\sum_{k=1}^{g} A_k^2 S^2(\bar{X}_k),$$

where $S_2(\bar{X}_k)$ = the variance for the mean number per tow in stratum k, which can be estimated as

$$S^2(\bar{X}_k) = \frac{\sum_{t=1}^{T_k}(X_{k,t} - \bar{X}_k)^2}{n_k(n_k - 1)}.$$

The mean length of the lobster population is estimated as

$$\bar{L} = \frac{\sum_{k=1}^{g} A_k \bar{C}_k}{\sum_{k=1}^{g} A_k \bar{X}_k}.$$

The average length fish per tow, $\bar{C}_k$, in the above equation is calculated as

$$\bar{C}_k = \frac{\sum_{t=1}^{T_k}\sum_{j=1}^{200} L_j X_{j,t,k}}{T_k},$$

where L_j = the lobster carapace size ranging from 1 to 200; and
$X_{j,t,k}$ = the number of the lobsters in size j, tow t, and stratum k.

The stratified mean number of lobsters of length j per tow, $\bar{X}_j$, can be estimated as

$$\bar{X}_j = \frac{1}{A}\sum_{k=1}^{g} A_k \bar{X}_{j,k},$$

where the mean number of lobsters of size j per tow, $\bar{X}_{j,k}$, is estimated as

$$\bar{X}_{j,k} = \sum_{t=1}^{T_k} \frac{X_{j,t,k}}{T_k}.$$

The above equations were used for both the original data (without any transformation) and the data transformed by using $\log(x+1)$. For results derived from the $\log(x+1)$ transformed data, a retransformation was done to retransform the log-based results to the results of the original scale by using the following equation:

$$U = \exp(Y + \sigma_U^2/2),$$

where Y = the statistics derived from $\log(x+1)$ transformed data;
U = is the re-transformed statistics; and
σ_U^2 = the population variance estimates as

$$\sigma_U^2 = \frac{1}{\sum_{k=1}^{T_k} A_k}\sum_{k=1}^{T_k}\left[A_k S_{Y_k}^2 + A_k\left(\bar{Y}_k - \frac{\sum_{k=1}^{T_k} A_k \bar{Y}_k}{\sum_{k=1}^{T_k} A_k}\right)^2\right],$$

where $S_{Y_k}^2$ and $\bar{Y}_k$ = the variance and mean value of $\log(x+1)$ transformed data in stratum k, respectively.

Using the above equations, we estimated the stratified mean number of lobsters per tow for original and $\log(x+1)$ transformed data, the stratified mean size frequency, and the stratified mean size of lobsters for the Maine inshore surveys. The average weight of lobsters for each tow was also calculated and then plotted against the average depth of the tow to identify if there was any size-depth dependent distribution. It should be noted that observations of zero lobsters occurred only for a small number of tows in the years covered in our study. Thus for the DMR inshore survey, there was no need to use methods such as delta transformation, which is often used in dealing with zero-inflated survey data with a large number of zero lobster catches.

The stratified mean number of lobsters per tow, stratified mean size frequency, and stratified mean size of lobsters for the NMFS survey program were obtained from the NMFS (Idoine[2]). Because of the large number

[2] Idoine, J. 2004. Personal commun. Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026.

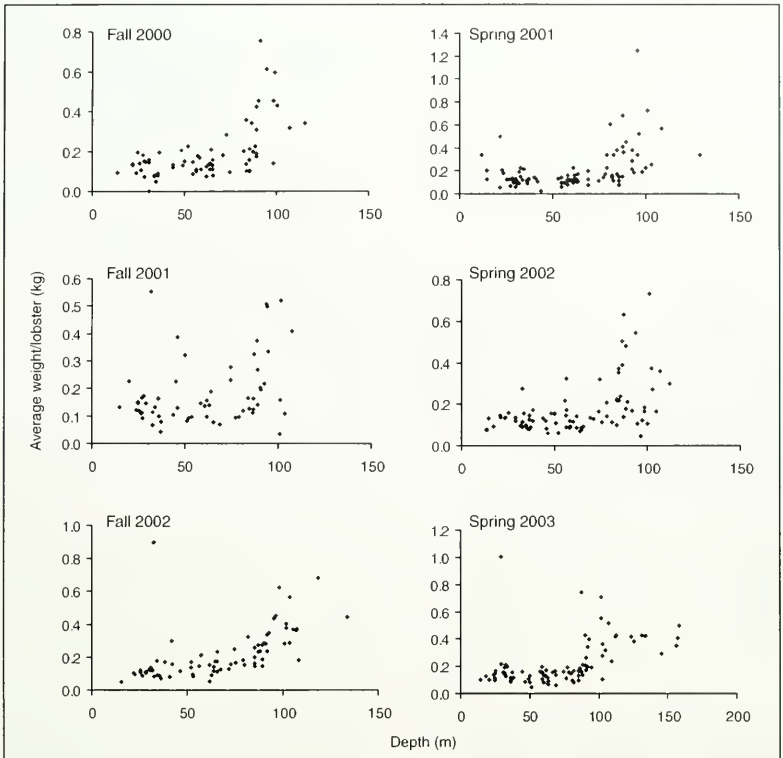

Figure 2

The changes in the average weight of American lobster (*Homarus americanus*) with the average depth of survey for each tow in each sampling season and year.

of tows with zero lobsters in the NMFS survey, a delta transformation was used to estimate the stratified mean of lobsters per tow. Because the DMR inshore survey program began in fall 2000, we used data from the NMFS survey program for the same time period only for our comparison of data. Currently the stock assessment uses only female data because females and males exhibit similar pattern; therefore we report results for females only in the present study.

Results

The average weight per lobster tended to be low and relatively constant for lobsters caught in the tows conducted in waters shallower than 73 m but increased greatly with increased depths (Fig. 2). The average carapace length for the first two depth strata, which were shallower than 72 m, were similar for each year and sampling season, but were much smaller than the average carapace length of lobsters in the third depth stratum which was deeper than 73 m (Table 1). For example, for the 2000 fall survey, the average lobster size for depth strata I and II were 61.9 and 64.4 mm—much smaller than 80 mm for stratum III. These distributional patterns in the lobster average weight and average size were consistent among years and seasons, indicating that lobsters inhabiting waters shallower than 73 m were mainly small individuals, whereas lobsters in waters deeper than 73 m were much larger than those in the shallow waters. A fourth depth stratum was used in the 2003 spring survey, where the average towing depth was 125 m. The average size of lobsters sampled in this stratum was 99.5 mm, which was similar to the stratified mean size of lobsters estimated in the NMFS survey program (Fig. 3).

There were no significant differences in size distributions among years in a given sampling season (i.e.,

Table 1

Summary of the mean carapace length of lobsters (*Homarus americanus*) and average survey depth for different depth strata in the inshore surveys. Roman numerals stand for depth strata: I=9–37 m; II=37–64 m; III=64–100 m; IV=>100 m). na=not available.

		Mean carapace length (mm)				Average depth (m)			
Year	Season	I	II	III	IV	I	II	III	IV
2000	fall	61.9	64.4	80.0	na	28.6	57.9	89.2	na
2001	fall	63.6	63.0	78.0	na	28.2	53.7	88.8	na
2002	fall	63.6	69.9	84.4	na	29.8	57.1	93.0	na
2001	spring	66.1	63.7	79.9	na	29.5	59.2	89.0	na
2002	spring	61.5	61.1	78.6	na	29.7	56.4	89.7	na
2003	spring	68.6	64.0	74.9	99.5	29.3	59.0	87.7	125.4

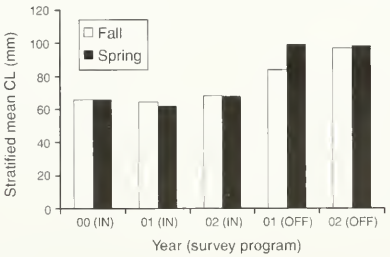

Figure 3

The stratified mean carapace length (CL) for American lobsters (*Homarus americanus*) for each sampling season and year for the Maine Department of Marine Resources inshore (IN) and the National Marine Fisheries Service offshore (OFF) survey programs. 00=2000; 01=2001; 02=2002.

either fall or spring survey) for the inshore survey (Fig. 4). For the NMFS survey, however, significant differences were found in size distributions between 2001 and 2002 in the fall surveys, but not between the two years in the spring surveys. The seasonal differences (i.e., spring vs. fall) in size distribution within a year were much larger than the between-year differences for the inshore fall or spring survey. For the NMFS survey, however, the seasonal differences in size distributions were large in 2001, but small in 2002 (Fig. 4). The large seasonal differences in a year compared to the between-year differences in a season in size distributions for the inshore survey indicate that seasonal factors are important in determining the size distribution of lobsters in the inshore waters. Such seasonal variability was not so clear for the offshore waters.

Large differences in size distributions were observed between the DMR inshore and NMFS surveys; the NMFS surveys consisted of lobsters of much larger sizes than those sampled inshore (Fig. 4). This finding may indicate that the inshore survey program had a limited coverage of the lobsters of large sizes, whereas the NMFS survey program had a limited coverage of the lobsters of small sizes. The size composition of lobsters from the NMFS survey had large variations. This result was probably due to the small number of lobsters caught in the NMFS survey. An increase in sample size could make the size composition curve smoother, and thus better defined. Compared with size composition of Amercan lobsters from the NMFS survey, size composition for the inshore survey was better defined, probably as a result of the larger number of lobsters caught in the inshore survey.

The stratified mean sizes of lobsters were similar among years for the same sampling season in the inshore survey (Fig. 3). For 2001, the stratified mean size in the fall survey was almost the same as that in the spring survey. For 2002, however, the stratified mean size in the fall survey was about 7 mm larger than that in the spring survey (Fig. 3). The stratified mean size of the 2001 fall survey was about 16 mm smaller than that of the 2001 spring survey (Fig. 3). The stratified mean size of lobsters in the NMFS survey was much larger than that of the inshore survey. This reconfirms the results derived from the comparisons of size distributions between the inshore and NMFS surveys (Fig. 4).

The abundance index derived from the inshore survey program revealed a consistent temporal pattern with original data or retransformed data (Table 2). For the original data and retransformed data, the fall inshore survey abundance index was the highest in 2001, followed closely by 2002, and the abundance index in 2000 was the lowest. For the log-transformed data, however, the differences among the three years were small (Table 2). For the spring survey, the abundance index in 2002 was much higher than the abundance indices in 2001 and 2003, and the abundance indices in 2001 and 2003 were similar (Table 2). The delta mean abundance indices of the NMFS survey program were higher in 2002

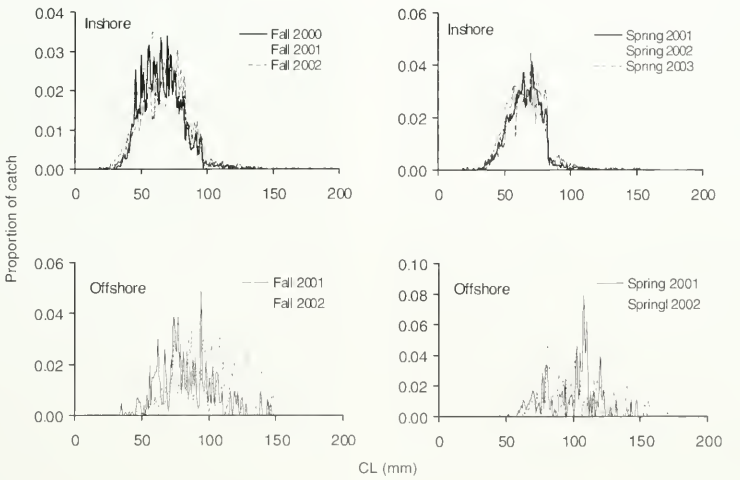

Figure 4

The size (of carapace [CL]) distributions for American lobsters (*Homarus americanus*) for each sampling season and year for the Maine Department of Marine Resources inshore and the National Marine Fisheries Service offshore survey programs.

Table 2

Estimates of the survey abundance index obtained from the original data and log(x+1) transformed data, and the retransformed abundance index derived from log(x+1) transformed data. "Lower B" and "upper B" are the lower and upper boundaries of the 95% confidence intervals.

		Statistics		Fall		Spring	
Index		2000	2001	2002	2001	2002	2003
Original (inshore)	Mean	55.5	68.5	64.1	22.6	49.2	21.2
	Lower B	32.7	45.1	51.7	16.4	34.7	15.8
	Upper B	78.2	91.9	76.5	28.8	63.6	26.7
Log(x+1)	Mean	2.9	2.9	3.1	2.1	2.7	2.2
transformed (inshore)	Lower B	2.6	2.5	2.8	1.9	2.4	1.8
	Upper B	3.2	3.3	3.5	2.4	3.0	2.6
Retransformed (inshore)	Mean	54.5	119.6	88.8	25.1	62.4	24.3
	Lower B	39.5	81.5	62.4	19.6	45.9	16.1
	Upper B	75.2	175.1	126.3	32.0	84.7	36.5
Delta mean (NMFS)	Mean		1.52	2.67	1.63	2.53	

than those in 2001 for both the fall and spring surveys. Thus, for fall, DMR inshore survey program had a different temporal pattern between 2001 and 2002, compared with the NMFS surveys, whereas for spring, the temporal pattern of 2001 and 2002 was same for the two sampling programs.

Discussions

Large differences were found in size compositions and mean sizes of lobsters between the DMR inshore and NMFS surveys. Such differences indicated that large lobsters are more likely to appear in the NMFS survey,

and small lobsters are more likely to appear in the inshore survey. This is true for both sampling seasons, fall and spring. Two possible hypotheses can be developed to explain such patterns: one is that large differences in size compositions exist in lobsters inhabiting the areas covered by the inshore and NMFS survey programs, and the other is that the observed differences in size compositions between the DMR inshore and NMFS surveys result from differences in gear selectivity for lobsters of different sizes. The first hypothesis implies that lobsters have size-dependent inshore-offshore distribution, namely that large lobsters tend to inhabit deep waters and small lobsters inhabit shallow waters. The second hypothesis implies that although lobsters may have no size-dependent inshore-offshore distribution, the NMFS survey gears are selective for large lobsters and the inshore survey gears are selective for small lobsters in the population. Such a difference in gear selectivity between the two programs may result from differences between the two sampling programs not only in sampling gears but in towing speed and duration.

In order to determine which hypothesis is more plausible, we evaluated size composition for a depth stratum covered by both the DMR inshore and NMFS surveys. In the 2003 spring inshore survey, the fourth depth stratum had an average depth of 125 m which overlapped depth ranges in the NMFS surveys. The average size of lobsters in the fourth depth stratum in the 2003 spring inshore survey was almost identical to the average size of lobsters in the NMFS survey (Table 1 and Fig. 3). This finding indicates that the inshore survey gears can, like the NMFS survey gears, catch large lobsters if they are present in the areas covered by the survey program. Likewise, the differences in the average size between the first three strata and the fourth stratum (Table 1) in the 2003 spring inshore survey are likely to result from a lack of large lobsters in the first three strata in the inshore surveys, rather than from gear selectivity. Thus, the differences in size composition of lobsters between the DMR and NMFS surveys are likely the result of the differences in the size composition of the lobster population between the areas covered by the inshore and NMFS surveys, rather than the result of sampling methods. Although our study could not exclude the impacts of possible differences in gear selectivity on the survey size compositions, the results of our study seem to support the first hypothesis that the lobsters have a size-dependent inshore-offshore distribution, where large lobsters are more likely to be found in deep waters and small lobsters are to be found in shallow inshore waters. Thus, the two sampling programs tend to cover different segments of the stock in the Gulf of Maine. In order to have an adequate representation of the lobster population, it is necessary to include data from both sampling programs to describe the lobster population dynamics in the Gulf of Maine.

The temporal changes in the abundance index in the spring surveys were rather consistent between the DMR and NMFS surveys and for data on the original and log scales. However, for the fall survey, the delta mean of the NMFS survey was consistent only with the mean of log-transformed data, but not with the mean of the original data and the mean retransformed data from the mean of log-transformed data (Table 2). This finding raises an interesting question regarding the type of data transformation we should choose and the potential impacts of each type on detecting temporal changes in the population abundance. A different choice of data transformation methods may lead to different interpretations of temporal variations in stock abundance.

If the size-dependent inshore-offshore distribution pattern is not taken into consideration in making stock assessments, the entire stock will not be managed. We may need a separate set of abundance indices and size compositions for the lobsters in the inshore and offshore waters to describe the population dynamics of lobsters of different size groups more accurately. The inclusion of only NMFS survey data or inshore survey data in the stock assessment may lead to errors in determining the status of the lobsters if the population dynamics of large lobsters is different from that of small lobsters. The blending of DMR and NMFS data into a single set of data may be a solution. However, whether such a set of data can describe the dynamics of the whole population depends upon whether the lobster population dynamics are consistent among different size classes and whether there is a large difference in gear selectivity and in catchability of the trawl gear. Large differences in the population dynamics of large and small lobsters and in the gear selectivity and catchability of DMR and NMFS trawls may make such blended data less desirable for describing the population dynamics with DMR-NMFS blended data. For example, a significant increase or decrease in the abundance of lobsters of prerecruiting sizes may not be well defined with the NMFS surveys or DMR-NMFS blended data. We recommend both sets of data from the DMR inshore and the NMFS surveys be used separately in the stock assessment to define the population dynamics of the lobsters in the Gulf of Maine more accurately.

Many fish species in the world exhibit a size-dependent distribution pattern similar to that of the American lobster in the Gulf of Maine. Their population abundance and size structure are often assessed by fisheries-independent survey programs. The information is then used in the assessment and management of these fish species. Because it is often difficult with large trawls to survey inshore areas where the majority of stocks are present, the fishery-independent survey may not provide adequate coverage of inshore areas that are productive and critical, in particular, to recruitment. Thus, it is highly likely that fish in inshore areas are not adequately represented in an offshore-focused survey, and this misrepresentation would lead to errors in data on stock-size structure. Such an error may, in turn, result in large errors in a stock assessment if an age- or length-based stock assessment model is used. We suggest that two sampling programs with different spatial focuses may help identify the problems associated with a sampling program that does encompass fish

size-dependent inshore-offshore distribution (or a size-dependent distribution that is related to depth or other environmental variables). The two sampling programs can greatly improve the quality and quantity of data collected in a fishery-independent program, leading to the improved assessment and management of fisheries. In the case where only one survey program can be conducted (e.g., due to budget limitation or time constraints, or both), we suggest that area-specific fishery landing data, together with depth or other environmental variables that influence fish distributions, be used in allocating sampling efforts in a random stratified survey.

Acknowledgments

We would like to thank R. Tetrault of T&R Fish Inc. for providing the vessels, Capt. Curtis Rice of the FV *Robert Michael* and Capt. Samuel Galli of the FV *Tara Lynn* for contributing to the project from the start. We also would like to thank V. Manfredi, J. Brown, K. Stepanek, and D. Grout for field assistance and data entry and preparation. L. Jacobson and J. Idoine of the Northeast Fisheries Science Center provided the NMFS survey information, which we appreciate greatly. The financial support of this study was provided by the NMFS, Maine Department of Marine Resources, Northeast Consortium, and Maine Sea Grant Program.

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Juvenile fish assemblages collected on unconsolidated sediments of the southeast United States continental shelf

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Abstract—Patterns were investigated in juvenile fish use of unconsolidated sediments on the southeast United States continental shelf off Georgia. Juvenile fish and environmental data were sampled at ten stations along a 110-km cross-shelf transect, including four stations surrounding Gray's Reef National Marine Sanctuary (Gray's Reef NMFS). Cross-shelf stations were sampled approximately quarterly from spring 2000 to winter 2002. Additional stations were sampled on three transects inshore of Gray's Reef NMS and four transects offshore of the Sanctuary during three cruises to investigate along-shelf patterns in the juvenile fish assemblages. Samples were collected in beam trawls, and 121 juvenile taxa, of which 33 were reef-associated species, were identified. Correspondence analysis on untransformed juvenile fish abundance indicated a cross-shelf gradient in assemblages, and the station groupings and assemblages varied seasonally. During the spring, fall, and winter, three cross-shelf regions were identified: inner-shelf, mid-shelf, and outer-shelf regions. In the summer, the shelf consisted of a single juvenile fish assemblage. Water depth was the primary environmental variable correlated with cross-shelf assemblages. However, salinity, density, and water column stratification also correlated with the distribution of assemblages during the spring, fall, and winter, and along with temperature likely influenced the distribution of juvenile fish. No along-shelf spatial patterns were found in the juvenile fish assemblages, but the along-shelf dimension sampled was small (~60 km). Our results revealed that a number of commercially and recreationally important species used unconsolidated sediments on the shelf off Georgia as juvenile habitat. We conclude that management efforts would be improved through a greater recognition of the importance of these habitats to fish production and the interconnectedness of multiple habitats in the southeast U.S. continental shelf ecosystem.

Manuscript submitted 26 October 2004 to the Scientific Editor's Office.

Manuscript approved for publication 25 August 2005 by the Scientific Editor.

Fish. Bull. 104:256–277 (2006).

Fisheries management has been rapidly evolving for the southeast United States with the development of a formal stock assessment process (i.e., SEDAR[1]), and the identification of essential fish habitat (EFH; SAFMC, 1998). Single-species management plans have been used as the basis for fisheries management along the southeast United States for decades, and EFH is just beginning to be incorporated into management plans (e.g., *Sargassum* and *Oculina* bank habitat of particular concern: FR, 2000). Globally, as fish stocks continue to decline (Botsford et al., 1997) and harvest shifts to new species (Pauly et al., 1998), interest in ecosystem management and implementation of MPAs in many areas, including the southeast U.S. continental shelf, is growing (SAFMC, 2001). Understanding how juvenile fish use habitat is important for both single-species fishery management and ecosystem approaches to fishery management. A description of habitat needs at each life history stage for species that represent the "significant food web" are also a recognized part of fishery ecosystem plans (NOAA[2]; CFEPTAP, 2004).

Adult population variability, in most species, is caused by variability in the survival of the early-life stages: egg, larval, and juvenile (Sissenwine, 1984; Rothschild, 1986). Survival of these early stages is influenced by both habitat quantity and quality (Gibson, 1994; Peterson, 2003). One approach to improving marine fisheries management is to incorporate habitat effects on early-life stage survival into stock assessments (Beck et al., 2001; Peterson, 2003). Determining how juvenile fish use habitat also benefits marine protected area (MPA) design and implementation. MPAs have been proposed to complement traditional fishery management practices by imposing site-specific rules to protect enclosed resources (Parrish, 1999; Dayton et al., 2000; Beck and Odaya, 2001). In some instances, MPAs provide benefits to outside areas through spillover effects (Roberts et al., 2001). MPAs may also provide a source of recruits to other nonprotected areas through planktonic transport (Cowen et al., 2000; Shanks et al., 2003). To be effective in protecting fishery resources, an MPA or a network of MPAs needs to encompass the habitats used by spe-

[1] SEDAR (Southeast Data Assessment and Review). 2002. Southeast Data Assessment and Review (SEDAR). South Atlantic Fishery Management Council, Charleston, SC. Website: http://www.sefsc.noaa.gov/sedar.jsp [Accessed on 19 October 2004.]

[2] NOAA (National Oceanic and Atmospheric Administration). 1999. Ecosystem-based fishery management. A report to Congress by the Ecosystems Principles Advisory Panel. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA.]

cies throughout their life cycle (Browman and Konstantinos, 2004).

Habitat use by juvenile fish has been studied extensively along the southeast United States, particularly for commercial and recreational species and structured habitats. For example, there is information available regarding the habitat use of specific estuarine (e.g., *Cynoscion nebulosus*: Thayer et al., 1999; paralichthid flounders: Walsh et al., 1999) and reef-associated species (e.g., *Mycteroperca microlepis*: Ross and Moser, 1995; *Lutjanus griseus*: Chester and Thayer, 1990; *Centropristis striata*: Lehnert and Allen, 2002). The importance of structural habitat to juvenile fish is also demonstrated by the consistent use of seagrass (Thayer et al., 1999), oyster reef (Meyer and Townsend, 2000), pelagic *Sargassum* (Moser et al., 1998), mangrove (Thayer et al., 1987), marsh (Hettler, 1989), and rocky reefs (Lindeman et al., 2000). Unconsolidated sediments in estuarine systems and from the surf-zone out into shallow coastal areas (<10 m) are also important juvenile habitat (estuarine: Burke et al., 1991; Walsh et al., 1999; surf-zone: Wenner and Sedberry, 1989; Ross and Lancaster, 2002).

Despite this large body of research, little is know about the use of unconsolidated sediments on the inner-, mid-, and outer-shelves of the southeast U.S. continental shelf. Unconsolidated sediment is not identified as EFH of the southeast U.S. (SAFMC, 1998), although it is identified in several fishery management plans (red drum, snapper-grouper, rock shrimp, royal red shrimp, coastal migratory pelagics, golden crab, spiny lobsters, and calico scallops). The only offshore habitats that currently have specific protection through their own fishery management plans are coral, coral reefs, live hard bottom, and pelagic *Sargassum* (Barnette[3]; FR, 2000). Research in other shelf ecosystems has identified unconsolidated sediments on the shelf as important juvenile habitat (Norcross et al., 1997; Steves et al., 2000; Sullivan et al., 2000; Johnson et al., 2001). Further, unconsolidated sediments on the southeast U.S. continental shelf cover a majority of the area (~60–80%; Parker et al., 1983), and likely serve as juvenile habitat for the more than 1200 fish species reported from the ecosystem (estimated from Kendall and Matarese, 1994). Thus, well-defined use of unconsolidated sediment habitat by juvenile fish is needed for sediment habitat to be incorporated into future fishery resource management on the southeast U.S. continental shelf.

Our purpose was to document juvenile fish habitat use and to examine the structure of juvenile fish assemblages in unconsolidated sediments off the Georgia coast region of the southeast U.S. continental shelf. Specific objectives were 1) to provide a list of species that use unconsolidated sediments on the shelf as juvenile habitat; 2) to determine which reef-associated species use unconsolidated sediments as juvenile habitat; and 3) to describe the relationships between the juvenile assemblages and environmental factors. The focus on reef fish was motivated largely by the emphasis to protect reef areas by using MPAs, as part of the management of the reef-associated snapper-grouper complex (SAFMC, 2001). If species of the reef-associated snapper-grouper complex use unconsolidated sediments during the juvenile stage, then protection of these habitats should be incorporated into the larger MPA effort.

Materials and methods

Study site

The continental shelf off the Georgia coast is the widest part (200 km) of the southeast shelf. The shelf in this region is gently sloping and comprises four depth zones (Menzel, 1993); inner-shelf (0–20 m); mid-shelf (20–40 m), outer-shelf (40–70 m), and shelf-edge (70–200 m). Each zone has different physical dynamics (Atkinson et al., 1985), climate (Blanton et al., 2003), and larval fish assemblages (Marancik et al., 2005). Demersal habitat consists of unconsolidated sediments, primarily medium to coarse quartz and carbonate sands (Nelson et al., 1999) interspersed with rocky reefs (Parker et al., 1983). Reefs of the southeast U.S. shelf range from no relief patchy live-bottom communities, to high-relief ledges. On the shelf off Georgia, rocky-reefs cover about 30% of the bottom (Parker et al., 1983). Rocky-reef habitats have a high diversity of invertebrate (Wenner et al., 1983) and vertebrate faunas (Chester et al., 1984; Parker and Mays, 1998; Lindeman et al., 2000). Located within the continental shelf off Georgia is the 56-km^2 Gray's Reef National Marine Sanctuary (Gray's Reef NMS, Fig. 1). The sanctuary depth ranges from 18 to 22 m and the benthic macrohabitat is mainly (~75%) unconsolidated sand sediments interspersed with patchy live-bottom and moderate relief (≤2 m) hard-bottom ledges (Parker et al., 1994). The adult reef fish community of the sanctuary is typical of other inner-shelf (<30 m) reefs of the South and North Carolina shelves (Chester et al., 1984; Parker et al., 1994).

Collection of juvenile fish and environmental data

Sampling of juvenile fish was conducted approximately quarterly from April 2000 through February 2002 (Table 1). Ten cross-shelf stations (stations 1–7), approximately 18.5 km apart, were sampled during most cruises (Fig. 1). Stations were missed on some cruises owing to weather and equipment failure (Table 1). The cross-shelf transect was 110 km long and stations were sampled on the inner-, mid-, and outer-shelf (10 to 50 m water depth). To avoid sampling within Gray's Reef NMS, four stations were placed immediately adjacent to the four sides of the sanctuary (stations 2.1–2.4). Additional

[3] Barnette, M. C. 2001. A review of the fishing gear utilized within the Southeast Region and their potential impacts on essential fish habitat. NOAA Tech. Memo. NMFS-SEFSC-449, 62 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA.]

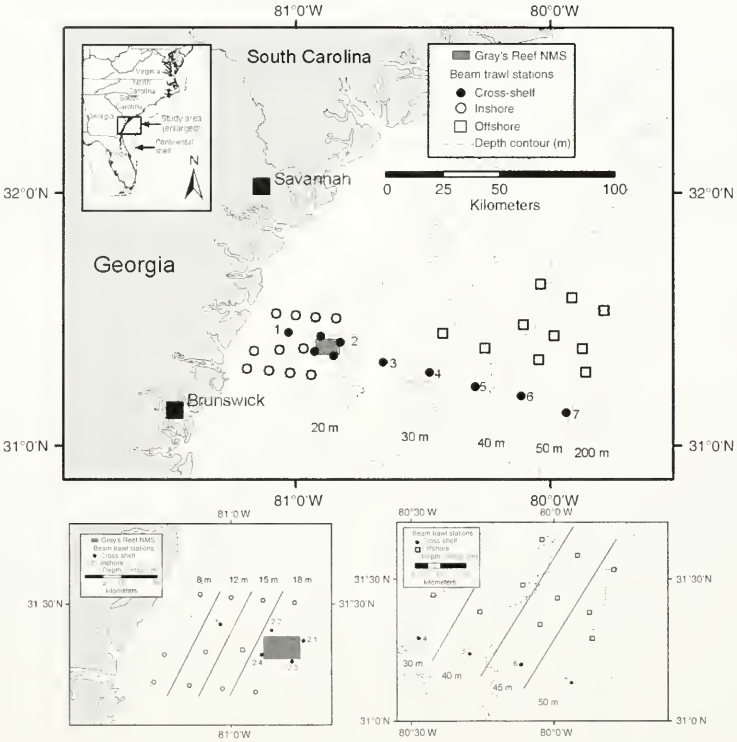

Figure 1

Maps of the study area showing cross-shelf beam trawl stations (black dots) at which juvenile fish and environmental sampling occurred quarterly from April 2000–February 2002 (see Table 1). Additional stations were sampled inshore (circles) and offshore (squares) of Gray's Reef NMS (see Table 1) (**A**). Station groups used in correspondence analysis of the inshore (**B**) and offshore (**C**) juvenile fish data sets are separated by solid lines and labeled.

stations were sampled along three transects inshore of Gray's Reef NMS and along four offshore transects during three cruises (Fig. 1 and Table 1). The benthic macrohabitat of the cross-shelf stations was determined by using a remotely operated vehicle (ROV, *Phantom* S2). The ROV was deployed off the starboard side of the ship. Approximately 30 m of the ROV tether was let out before the tether was attached to a 45-kg weight. The weight was lowered to 3 m above the bottom and the ship was allowed to drift. During April 2000, two 15-min drifts were made at eight of the ten cross-shelf stations. Because of inclement weather, no drifts were conducted at the inner- or outer-most stations. Video (HI-8 mm) was recorded of each drift.

Concurrent fish and hydrographic measurements were taken to examine the relationship between juvenile fish assemblages and the environment. At each station, temperature, salinity, density, and water depth were measured from the water's surface to one meter above the bottom with a Seabird CTD (SBE19, Seabird Electronics, Inc., Bellevue, WA). Juvenile fish were collected at each station by using a 2-m beam trawl with a 6-mm mesh body and a 3-mm mesh tail bag. Two kilogram weights were added to each skid of a standard 2-m beam trawl (Kuipers, 1975) to ensure that the trawl stayed on the bottom. Three 5-min bottom tows were made at each station. Samples were sorted on deck and fish and invertebrates were preserved in 95% ethanol.

Preparation of fish data

All beam trawl samples were sorted and fish were identified to the lowest possible taxonomic level by using previously published descriptions (e.g., Able and Fahay,

Table 1

Number of beam trawl stations sampled off the coast of Georgia for juvenile fish. Station groups correspond to the station locations in Figure 1.

				Station group		
Year	Month	Dates	Season	Cross-shelf	Inshore	Offshore
2000	April	24–27	spring	9		
	June	19–22	summer	9		
	August	15–17	summer	9		
	October	03–07	fall	10		
2001	Jan/Feb	30–01	wnter	10		
	March	21–23	winter	10		
	Apr/May	30–04	spring	10	11	
	June	04–09	summer	10		
	August	03–06	summer	10		
	September	07–09	fall			6
	October	11–13	fall	10		
2002	February	08–13	winter	10	10	10

1998; Munroe, 1998). Identification to species was not possible for all fish. Taxa were separated into larval, juvenile, and adult age classes according to life-history characteristics from the literature and standard length distributions (SL, mm) from the beam trawl collections. Fish were classified as larvae if fin development was not complete (and defined as "larvae at settlement stage" when fin formation was complete and pigmentation incomplete; fish were classified as juveniles when pigmentation was complete, and were classified as adults if they exceeded the reported minimum SL for sexual maturity. Because the mesh of the beam trawl is large enough to extrude larvae and less efficient at catching large (>150 mm SL) fish (Kuipers, 1975), analyses in this study were conducted only on settlement and juvenile stages, which were combined and referred to as juveniles. Taxa were also classified as not reef-associated, strongly reef-associated or weakly reef-associated based on habitat-use information (Chester et al., 1984; Humann, 1994; Parker et al., 1994; Parker and Mays, 1998; Lindeman et al., 2000). Taxa found predominantly on rocky-reefs (e.g., *Centropristis striata*) were classified as strongly reef-associated. Those that use rocky-reefs and other habitats (e.g., *Diplectrum formosum*) were classified as weakly reef-associated.

Standard catch per unit of effort (CPUE, fish/5-min bottom tow) was calculated for each taxon. CPUE for each taxon at each station was the average of all replicate tows. Three juvenile stage data sets (i.e., cross-shelf, inshore, and offshore) were compiled by using data from the station groups (Table 1, Fig. 1): the cross-shelf data set consisted of data from stations one through seven (Fig. 1A); the inshore data set consisted of data from stations predominately inside the 20-m isobath (Fig. 1B), and the offshore data set consisted of date from stations >30 m in depth (Fig. 1C).

For statistical analyses, the three data sets were subdivided into two groups so that rare taxa would not greatly influence the classification of assemblages. The first group consisted only of abundant taxa, and the second group included abundant and rare taxa. Cross-shelf and offshore data sets were subdivided into taxa that made up at least 10% (abundant) and 1% (abundant and rare) of the collections at any one station. The inshore data set was subdivided at 5% and 1% levels. The data sets were further condensed by eliminating all taxa not identified to species level with the exception of *Stenotomus* sp. and *Rypticus* sp. which were probably single species. Several abundant taxa were excluded from the analysis because they were only identified to genus and have multiple species common in the area, and each species may differ in distribution: i.e., *Etropus* spp. (4 species), *Prionotus* spp. (14 species), *Sphoeroides* spp. (11 species), *Microgobius* spp. (3 species), and *Bothus* spp. (3 species). As a result, the numbers of taxa in the rare and abundant data sets used in analyses were as follows: cross-shelf 82 (rare) and 28 (abundant) (Table 2); inshore 28 and 13 (Table 3), and offshore 51 and 17 (Table 4).

Preparation of environmental data

Season and five environmental (or hydrographic) variables were chosen in an attempt to explain variation in the juvenile fish data. Cruises were assigned to one of four seasons (Table 1) based on wind (Atkinson et al., 1985) and temperature regimes (Marancik et al., 2005). Environmental variables were calculated as in Marancik et al. (2005). Briefly, CTD measurements of temperature (°C) and salinity were used to derive density (σ_t, Kg/m^3). Bottom temperature, salinity, and density were used in the multivariate analyses with juvenile fish because benthic habitats were sampled and bottom values were

Table 2

Taxa collected by beam trawl during two years of sampling (April 2000–February 2002) at the cross-shelf stations (see Fig. 1A) off the coast of Georgia, and used in correspondence analysis. Mean and standard deviation (SD) of catch per unit of effort (CPUE) were calculated for the entire data set. Taxa that constituted one or ten percent of any one station were used in the analyses, and an asterisk next to a taxon indicates that it was in the 10% data set. Seasonal juvenile assemblages from correspondence analysis are shown (I= inner-shelf; I/M=inner-/mid-shelf; M=mid-shelf; O-outer-shelf; and S=entire shelf; S). Taxa in bold indicate reef-associated species.

		CPUE		Seasonal juvenile assemblage			
Family	Taxon	Mean	SD	Spring	Summer	Fall	Winter
Elopidae	*Elops saurus*	0.010	0.097		S		M
Ophichthidae	*Ophichthus gomesii*	0.003	0.056		S		
	Ophichthus ocellatus	0.021	0.155	I/M	S	M	M
Congridae	*Ariosoma balearicum**	0.163	0.479	I/M	S	M	M
Clupeidae	*Brevoortia tyrannus*	0.019	0.134				M
	Etrumeus teres	0.006	0.080				M
	Sardinella aurita	0.003	0.056		S		
Engraulididae	*Anchoa hepsetus**	0.303	1.313	I/M	S	M	
	Anchoa lamprotaena	0.013	0.237			M	
Argentinidae	*Argentina striata*	0.006	0.080				O
Synodontidae	*Synodus foetens**	0.746	1.626	I/M, O	S	M	M
	Synodus poeyi	0.048	0.487	O			
	Trachinocephalus myops	0.103	0.388	O	S	M,O	O
Gadidae	*Urophycis regia**	0.234	0.759	I/M			M
Ophidiidae	*Ophidion selenops**	2.185	4.844	I/M	S	M	M
	*Otophidium omostigmum**	0.364	1.190	O	S	O	M
Batrachoididae	*Porichtys plectrodon*	0.006	0.072			M	
Antennariidae	***Antennarius radiosus***	0.006	0.080				M, O
Ogcocephalidae	*Halicutichthys aculeatus*	0.019	0.137	O	S		
	Ogcocephalus nasutus	0.024	0.150	I/M	S		I
Exocoetidae	*Hemiramphus brasilieusis*	0.003	0.056		S		
	Hirundichthys affinis	0.022	0.169		S	M	
Syngnathidae	*Hippocampus erectus*	0.052	0.233	I/M	S	M	I,M,O
	*Syngnathus scovelli**	0.025	0.192		S	I	
	Syngnathus springeri	0.025	0.158	I/M	S		M
Scorpaenidae	***Scorpaena dispar***	0.019	0.161		S	M	
	Scorpaena plumieri*	0.080	0.332	I/M	S	M	M
Triglidae	*Bellator brachychir*	0.006	0.074		S	O	
	Bellator militaris	0.006	0.073	O	S		
	*Prionotus carolinus**	1.047	2.970	I/M	S	M	M
	Prionotus ophryas	0.003	0.056		S		
	Prionotus scitulus	0.022	0.146				M
Serranidae	***Centropristis ocyurus****	0.167	1.344	O	S		O
	Centropristis striata	0.022	0.186	I/M	S		
	Diplectrum formosum*	1.556	3.659	O	S	M,O	M
	Serraniculus pumilio	0.180	0.817	I/M	S	M	M
	Serranus phoebe*	0.085	0.466	O	S	O	O
Priacanthidae	***Priacanthus arenatus***	0.003	0.056		S		
Apogonidae	***Pristigenys alta***	0.016	0.123		S	M	
	Apogon pseudomaculatus	0.012	0.108		S		
Carangidae	*Caranx bartholomaei*	0.003	0.051	O			
	Chloroscombrus chrysurus	0.014	0.124		S	M	
	Decapterus macarellus	0.006	0.080	O			M
	*Decapterus punctatus**	0.022	0.218		S		M
	Trachurus lathomi	0.003	0.054	I/M			
Lutjanidae	***Lutjanus analis***	0.003	0.056		S		

continued

Table 2 (continued)

Family	Taxon	CPUE		Seasonal juvenile assemblage			
		Mean	SD	Spring	Summer	Fall	Winter
Haemulidae	***Haemulon aurolineatum****	0.022	0.214		S	O	
Sparidae	***Stenotomus* sp.***	0.119	0.811	I/M	S	M	M
	Lagodon rhomboides	0.016	0.149				M
Sciaenidae	*Cynosion nothus*	0.009	0.110			M	
	Cynosion regalis	0.011	0.118			M	
	*Larimus fasciatus**	0.036	0.363			I	
	*Leiostomus xanthurus**	0.621	3.752				I
	Menticirrhus americanus	0.013	0.185			I	
Mugilidae	*Mugil cephalus**	0.051	0.469				O
	Mugil curema	0.010	0.099				M
Labridae	***Halichoeres bivattatus***	0.006	0.113		S		
	Xyrichtys novacula	0.003	0.056		S		
Uranoscopidae	*Kathetostoma albigutta*	0.003	0.056				M
Dactyloscopidae	*Dactyloscopus moorei**	0.837	2.329	I/M	S	M	M
Blenniidae	*Hypleurochilus geminatus*	0.010	0.126	I/M	S		
	Parablennius marmoreus*	0.006	0.080		S		
Callionymidae	*Diplogrammus pauciradiatus**	0.025	0.174		S		
Gobiidae	*Ioglossus calliurus*	0.003	0.047	O	S		
Stromateidae	*Peprilus triacanthus*	0.038	0.218	I/M			M
Bothidae	*Bothus lunatus*	0.006	0.080	O			O
	Bothus ocellatus	0.021	0.155		S	M	O
	*Bothus robinsi**	0.497	1.643	O	S	M	O
Paralichthyidae	*Ancylopsetta quadrocellata*	0.063	0.300				M
	Citharichthys macrops	0.096	0.475	I/M	S	M	M
	Cyclopsetta fimbriata	0.031	0.184	O	S	M	
	*Syacium papillosum**	0.042	0.282	I/M	S	O	
Soleidae	*Gymnachirus melas**	0.019	0.134	O	S		
Cynoglossidae	*Symphurus diomedeanus*	0.010	0.126	O			
	*Symphurus minor**	0.519	1.801	O	S	O	O
	Symphurus parvus	0.016	0.125	O	S		
	Symphurus plagiusa	0.006	0.113		S		
	*Symphurus urospilus**	0.324	0.806	I/M	S	M	M
Balistidae	***Aluterus schoepfi***	0.006	0.076		S	M	
	*Monocanthus hispidus**	0.504	1.424	I/M	S	M	O
	Monocanthus setifer	0.003	0.047			O	
Ostraciidae	***Lactophyrs quadricornis***	0.005	0.068		S		

highly correlated with the average water column and surface variables (Marancik et al., 2005). Vertical stratification was estimated by using Simpson's stratification parameter (Simpson and James, 1985), Φ (joules/m^3), which is a measure of the resistance of water to mixing (higher numbers signify higher resistance to mixing).

Data Analyses

Correspondence analysis (CA) and canonical correspondence analysis (CCA) were performed by using the statistical package CANOCO (ter Braak and Smilauer, 2002). Using the cross-shelf, inshore, and offshore data sets, we had seven objectives: 1) to describe the cross-shelf patterns in the juvenile fish assemblages; 2) to identify the species associated with the assemblages including the reef-associated species that contribute to these assemblages; 3) to describe the relationship among cross-shelf patterns in the assemblages and environmental variables; 4) to describe the seasonal patterns in the assemblages; 5) to determine the relation between seasonal assemblages and environmental variables; 6) to describe the along-shelf and cross-shelf patterns in the inshore data set; and 7) to describe the along-shelf and cross-shelf patterns in the offshore data set.

Correspondence analysis was used to define juvenile fish assemblages and to explore the factors that influence distribution of assemblages on the shelf off

Table 3

Taxa collected by beam trawl during spring and winter sampling at stations inshore of Gray's Reef National Marine Sanctuary (see Fig. 1B), and used in correspondence analysis. Mean and standard deviation (SD) of catch per unit of effort (CPUE) were calculated for the entire data set. Taxa that constituted one or five percent of any one station were used in the analyses, and an asterisk next to a taxon indicates that it was in the 5% data set. Station depth groups for each season for juvenile assemblages, as determined from correspondence analysis, are shown. Taxa in bold indicate reef-associated species.

		CPUE		Juvenile assemblage	
Family	Taxon	Mean	SD	Spring	Winter
Congridae	*Ariosoma balearicum**	0.022	0.147	12–15 m	
Clupeidae	*Sardinella aurita*	0.011	0.105	12–15 m	
Engraulididae	*Anchoa hepsetus**	0.613	5.135	8 m	8 m
	Anchoa lamprotaena	0.022	0.147	8 m	8 m
Synodontidae	*Synodus foetens**	0.416	1.525	12–15 m	12–15 m
Gadidae	*Urophycis regia**	0.718	1.176	12–15 m	12–15 m
Ophidiidae	*Ophidion selenops**	0.794	1.867	12–15 m	12–15 m
Ogcocephalidae	*Ogcocephalus nasutus*	0.011	0.105	12–15 m	
Syngnathidae	*Hippocampus erectus*	0.098	0.333	12–15 m	12–15 m
Scorpaenidae	***Scorpaena plumieri***	0.044	0.206	12–15 m	12–15 m
Triglidae	*Prionotus carolinus**	2.227	2.939	12–15 m	12–15 m
	Prionotus scitulus	0.122	0.332	12–15 m	
Serranidae	***Centropristis ocyurus***	0.022	0.147	12–15 m	
	Diplectrum formosum*	0.099	0.366	12–15 m	12–15 m
Sparidae	***Stenotomus* sp.***	0.261	0.949	12–15 m	12–15 m
Sciaenidae	*Leiostomus xanthurus**	14.053	46.103	8 m	
	Stellifer laceolatus	0.022	0.210	8 m	
Mullidae	*Upeneus parvus*	0.011	0.105	12–15 m	
Dactyloscopidae	*Dactyloscopus moorei**	0.545	1.108	12–15 m	12–15 m
Gobiidae	*Gobiosoma bosci*	0.053	0.303	12–15 m	
Stromateidae	*Peprilus triacanthus**	0.076	0.370	12–15 m	
Bothidae	*Bothus ocellatus*	0.010	0.095	12–15 m	
Paralichthyidae	*Ancylopsetta quadrocellata*	0.344	0.604	8 m	12–15 m
	Citharichthys macrops	0.088	0.353	8 m	12–15 m
Cynoglossidae	*Symphurus plagiusa**	0.112	0.538	8 m	
	Symphurus urospilus	0.109	0.403	12–15 m	12–15 m
Balistidae	*Monacanthus hispidus**	0.154	0.445	12–15 m	12–15 m
Ostraciidae	***Lactophyrs quadricornis***	0.011	0.105	8 m	

the coast of Georgia. CA arranges stations and species along gradients (Greenacre, 1984), creating a low-dimensional map (an ordination). Points that occur in close proximity can be considered to have similar species composition and abundance. Points that occur on the same dimension define gradients in the data. The eigenvalues, which are a relative measure of the amount of variance explained by each CA dimension (ter Braak and Smilauer, 2002), were used to determine the number of dimensions that best described the data. CA on untransformed CPUE data was used to define assemblages for the cross-shelf, inshore, and offshore data sets in relation to season.

Canonical correspondence analysis, which incorporates environmental variables by aligning species and station data along environmental gradients, was used to explore the relationship between juvenile assemblages and the environment. The species-environment correlation is a measure of the strength of the relation between the species data and the environmental data for each CCA dimension (ter Braak and Smilauer, 2002). The product of the species-environment correlation and the eigenvalue can be used to describe the variance in the data. CCA on untransformed CPUE data and standardized environmental data was used to explore the relation between the assemblages and environment for the cross-shelf, inshore, and offshore data sets in relation to season. Environmental data were standardized to a mean of zero and a standard deviation of one.

Results

Habitat characterization

The environmental variables showed the typical seasonal and depth patterns across the shelf (Fig. 2). During the spring, bottom water temperature was near 20°C

Table 4

Taxa collected by beam trawl during fall and winter sampling at stations offshore of Gray's Reef National Marine Sanctuary (see Fig. 1C), and used in correspondence analysis. Mean and standard deviation (SD) of catch per unit of effort (CPUE) were calculated for the entire data set. Taxa that constituted one or ten percent of any one station were used in the analyses, and an asterisk next to a taxon indicates that it was in the 10% data set. Station depth groups for each season for juvenile assemblages, as determined from correspondence analysis, are shown. Taxa in bold indicate reef-associated species.

		CPUE		Juvenile assemblage	
Family	Taxon	Mean	SD	Spring	Winter
Muraenidae	*Gymnothorax saxicola*	0.024	0.155	50 m	
Ophichthidae	*Ophichthus gomesii*	0.036	0.246	30–45 m	
Congridae	Ariosoma balearicum	0.183	0.485	30–45 m	50 m
Synodontidae	*Synodus foetens**	0.410	0.980	30–45 m	30–45 m
	Trachinocephalus myops	0.147	0.391	30–45 m	30–45 m
Ophidiidae	*Ophidion selenops**	0.813	2.289	30–45 m	30–45 m
	*Otophidium omostigmum**	0.957	1.401	50 m	30–45 m
Batrachoididae	*Porichtys plectrodon*	0.012	0.105	50 m	
Antennariidae	***Antennarius ocellatus***	0.012	0.109	50 m	
	Antennarius radiosus	0.039	0.203	50 m	
Ogcocephalidae	*Ogcocephalus nasutus*	0.059	0.233	30–45 m	
	Ogcocephalus parvus	0.024	0.154	50 m	
Syngnathidae	*Hippocampus erectus*	0.024	0.154	50 m	50 m
Scorpaenidae	***Scorpaena dispar****	0.152	0.989	50 m	50 m
	Scorpaena plumieri	0.137	0.510	30–45 m	50 m
Triglidae	*Bellator brachychir*	0.012	0.109	30–45 m	
	*Prionotus carolinus**	0.360	0.785	30–45 m	30–45 m
	Prionotus scitulus	0.024	0.153	30–45 m	
Serranidae	***Centropristis ocyurus****	0.998	2.381	50 m	50 m
	Diplectrum formosum*	2.305	4.132	30–45 m	30–45 m
	Epinephelus niveatus	0.024	0.155	50 m	30–45 m
	Serraniculus pumilio*	0.206	0.579	50 m	30–45 m
	Serranus phoebe*	0.857	3.515	50 m	50 m
	Serranus subligarius	0.037	0.331	50 m	
Grammistidae	***Rypticus* sp.***	0.239	1.330	50 m	50 m
	Rypticus bistrispinus*	0.280	1.336	50 m	
Priacanthidae	***Pristigenys alta***	0.049	0.217	50 m	
Apogonidae	***Apogon maculatus****	0.314	1.525	50 m	
	Apogon pseudomaculatus	0.107	0.439	30–45 m	50 m
Haemulidae	***Haemulon aurolineatum***	0.035	0.233	30–45 m	
Sparidae	***Stenotomus* sp.**	0.049	0.267	30–45 m	
Mugilidae	*Mugil cephalus*	0.024	0.221	30–45 m	
	Mugil curema	0.037	0.192	30–45 m	
Labridae	***Halichoeres bivittatus***	0.015	0.133	50 m	
Dactyloscopidae	*Dactyloscopus moorei*	0.049	0.266	30–45 m	
Blenniidae	*Hypleurochilus geminatus*	0.073	0.262	50 m	50 m
	Parablennius marmoreus	0.024	0.221	30–45 m	
Callionymidae	*Diplogrammus pauciradiatus*	0.048	0.212	50 m	30–45 m
Bothidae	*Bothus ocellatus**	0.143	0.701	30–45 m	50 m
	*Bothus robinsi**	0.665	1.145	30–45 m	30–45 m
Paralichthyidae	*Ancylopsetta quadrocellata*	0.060	0.284	30–45 m	
	Citharichthys macrops	0.024	0.152	30–45 m	
	Cyclopsetta fimbriata	0.095	0.394	30–45 m	
	Syacium papillosum	0.087	0.329	30–45 m	
Cynoglossidae	*Symphurus minor**	2.047	3.593	30–45 m	30–45 m
	*Symphurus urospilus**	0.194	0.501	30–45 m	30–45 m
Balistidae	***Cantherhines pullus***	0.061	0.287	50 m	
	Monocanthus ciliatus	0.012	0.110	50 m	
	*Monocanthus hispidus**	0.891	2.057	30–45 m	30–45 m
	Monocanthus setifer	0.012	0.110	50 m	
Ostraciidae	***Lactophyrs quadricornis***	0.012	0.108	30–45 m	

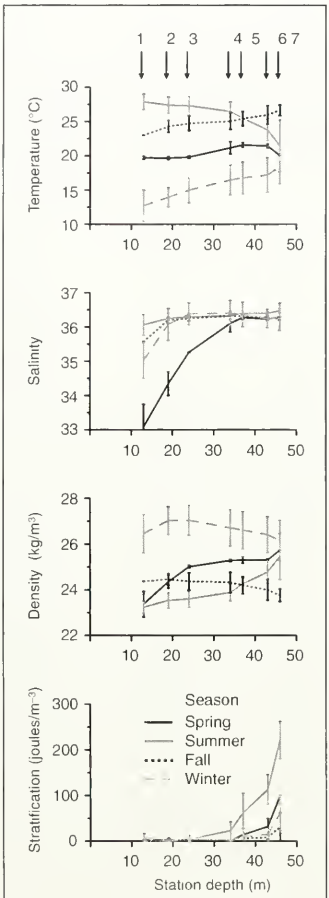

Figure 2

Seasonal average (SD) bottom temperature in °C (**A**) salinity (**B**), density (σ_t, Kg/m^3) (**C**) and stratification (Φ, joules/m^3) (**D**) across the coast off Georgia. The station numbers across the top correspond to the cross-shelf stations shown in Figure 1.

across the entire shelf (Fig. 2A). In the summer, bottom waters were warmest on the inner-shelf and cooler on the outer-shelf (Fig. 2A). Average fall bottom water temperature was intermediate between that of spring and summer and was warmest on the outer-shelf (Fig. 2A). The lowest bottom water temperatures were measured during the winter on the inner-shelf (Fig. 2A). Bottom salinity was lowest on the inner-shelf during all seasons (Fig. 2B). Bottom salinity was also low on the inner- and mid-shelves during the spring and rose to near 36 psu on the outer-shelf (Fig. 2B). During the summer, fall, and winter the mid- and outer-shelf bottom salinities remained near 36 psu (Fig. 2B). Bottom water density reflected the seasonal and cross-shelf patterns in temperature and salinity (Fig. 2C). Bottom water density was greatest during the winter when water temperatures were the lowest (Fig. 2C). In the spring, a cross-shelf pattern occurred and density was lowest inshore (Fig. 2C). During summer bottom water density was lowest inshore, where the water temperatures were low (Fig. 2C). There was no cross-shelf density pattern in the fall (Fig. 2C). Water column stratification was greatest during the summer and Simpson's stratification numbers were always higher on the outer-shelf (Fig. 2D). The low stratification numbers on the inner- and mid-shelves (Fig. 2D) indicated that there was a high probability of vertical mixing in all seasons.

Video analysis of the ROV tows indicated that the cross-shelf bottom on the continental shelf off the coast of Georgia consisted predominately of unconsolidated sand sediments. Hard-bottom (rock rubble) was seen in one video frame at station 2.3, on the southern edge of the Gray's Reef NMS. No ROV data were collected at the inner- or outermost stations; however, no hard-bottom has been reported from either station (SEAMAP-SA, 2001). These data indicate that unconsolidated sediments were sampled.

Cross-shelf patterns in the juvenile fish assemblages

One hundred eighty one taxa were collected with the beam trawl, and of these, 121 were classified as juveniles (Appendix). Twelve strongly reef-associated species and 21 weakly reef-associated species were collected. The assemblages exhibited a cross-shelf gradient and the station groupings varied seasonally (Fig. 3). CA of both the 10% and 1% data sets resulted in the same overall patterns; however, rare species frequently were found between station groups in the ordination. During the spring, there were two cross-shelf station groups that overlapped at station 4 (Fig. 3A), an inner and mid-shelf group (stations 1–4), mainly inshore of the 30-m isobath, and an outer-shelf group (stations 4–7). Eigenvalues of the CA showed that the separation of the two groups was mainly along the first dimension (Table 5). During the summer, there was little cross-shelf pattern in the assemblages. The only exception was station 2.3, which was distinct from all other stations because live bottom was sampled at that station (Fig. 3B). When this station was removed from the analysis, there was no cross-shelf pattern in the summer data set (Fig. 3C). Three cross-shelf station groups were present in the fall (Fig. 3D): inner-shelf (station 1), mid-shelf (stations 2–5), and outer-shelf (stations 6–7). Separation of the groups was predominately along the first dimension (Table 5), which separated the inner- and mid-shelf station groups from the outer-shelf station group. During the winter, there was a cross-shelf gradient in the juvenile fish assem-

blages and the three overlapping groups were not as distinct as they were in spring or fall (Fig. 3, E and F). The species composition and abundance at station 7 from January 2001 was dissimilar from the rest of the winter samples (Fig. 3E) and generated a high eigenvalue for the second dimension (Table 5). The cross-shelf gradient along the first dimension had the highest eigenvalue (Table 5) in the winter; the first dimension showed three cross-shelf groups (Fig. 3F): an inner-shelf group (stations 1–2), a mid-shelf group (stations 2–5), and an outer-shelf group (stations 4–7).

Species composition of juvenile fish assemblages

Five seasonal juvenile fish assemblages were associated with the cross-shelf station groups (Fig. 4, Table 2). The cross-shelf distribution of juveniles was related to adult distribution patterns and habitat use (Appendix). During the spring, the inner- and mid-shelf assemblage comprised species that are found in estuarine, coastal, and open-shelf habitats as adults (Fig. 4A, Appendix). *Synodus foetens* fell between the two station groups on the ordination, and was found in the both assemblages (Fig 4A). The outer-shelf assemblage was predominately coastal and open-shelf species (Fig. 4A, Appendix). Three reef-associated species were present in both assemblages (Table 2).

Eighteen juvenile reef-associated species were collected during the summer (Table 2). Six species (*Centropristis striata, Apogon pseudomaculatus, Haemulon aurolineatum, Stenotomus* sp., *Halichoeres bivittatus,* and *Parablennius marmoreus*) were collected in June 2001 at station 2.3, when sampling was conducted over live-bottom. Sixteen of the 56 species from the summer sampling were collected solely during this season, and overall, the entire shelf was considered a single assemblage (Table 2).

Only estuarine and coastal species were observed in the inner-shelf assemblage during the fall (Fig. 4B, Table 2). The greatest number of species was observed in the mid-shelf assemblage (Fig. 4B, Table 2), which consisted of a mixture of estuarine, coastal, and open-shelf species (Fig. 4B, Appendix). *Diplectrum formosum* was collected from stations 2 to 7 and was in both the mid- and outer-shelf assemblages (Fig 4B). The outer-shelf assemblage consisted of only coastal and open-shelf species (Fig. 4B, Appendix). Seven reef-associated species were present in mid- to outer-shelf assemblages during the fall (Table 2).

There was a cross-shelf gradient in the winter juvenile fish assemblages that was in-

Figure 3

Correspondence analysis (CA) ordinations (portraying the first and second dimension scores) of the 10% cross-shelf data set showing station groups in each season; spring (**A**), summer (**B**), summer without station 2.3 (**C**), fall (**D**), winter (**E**), and winter without station 7 (**F**). The cross-shelf station groups were identified within each season. Solid lines enclose the boundary of each station group with three or more stations. Station groups comprising one or two stations are not enclosed by a solid line. Each station group is labeled and identified by a different symbol. The dashed lines intersect at the origin of the plot. Analyses were conducted by using juvenile fish abundance data only. Data from each cruise within a season are shown together.

Table 5

Eigenvalues and species–environment correlations ($r2$) for each axis analyzed (correspondence analysis [CA] and canonical correspondence analysis [CCA]) by season and the entire year. A sharp drop in the eigenvalue marks the axes that explain most of the data. Eigenvalues alone explain the variance in the data for CA. The product of the species-environment correlation and the eigenvalue explains the variance in the data for CCA.

		CA axis				CCA axis			
Season		1	2	3	4	1	2	3	4
Spring	Eigenvalue	0.574	0.326	0.273	0.251	0.538	0.292	0.172	0.052
	r^2					0.971	0.962	0.959	0.577
Summer	Eigenvalue	0.461	0.389	0.350	0.303	0.248	0.160	0.123	0.049
	r^2					0.857	0.742	0.684	0.422
Fall	Eigenvalue	0.604	0.376	0.275	0.224	0.447	0.301	0.121	0.090
	r^2					0.910	0.899	0.846	0.765
Winter	Eigenvalue	0.669	0.644	0.492	0.414	0.531	0.306	0.181	0.118
	r^2					0.930	0.862	0.669	0.625
Year	Eigenvalue	0.698	0.507	0.499	0.394	0.169	0.125	0.102	0.089
	r^2					0.606	0.628	0.615	0.522

Table 6

The P values from a Monte Carlo permutation test on the environmental variables for each season. Significant P values ($P<0.05$) are in bold.

	Season			
Variable	Spring	Summer	Fall	Winter
Depth (m)	**0.002**	0.918	**0.002**	**0.002**
Stratification	**0.002**	**0.002**	0.622	0.178
Bottom temperature	0.410	0.138	0.094	0.070
Bottom salinity	1.000	0.160	**0.020**	0.316
Bottom density	**0.034**	0.848	0.102	**0.020**

fluenced by the single station 7 (Fig. 3E), which had a high abundance of *Monacanthus hispidus*. *Bothus ocellatus* and *B. lunatus* were also collected only at this station (Table 2). The inner-shelf consisted of one dominant species (Fig. 4C), and the mid-shelf had the greatest number of species (Fig. 4C, Table 2). The outer-shelf assemblage consisted of estuarine, coastal, and open-shelf species (Fig. 4C). Six reef-associated species were found in the mid- and outer-shelf assemblages. The distributions of species in all three winter assemblages indicated cross-shelf mixing. An open-shelf species, *Ogcocephalus nasutus*, was present in the inner-shelf assemblage and *Mugil cephalus*, which uses estuaries as adults, was present in the outer-shelf assemblage (Table 2, Appendix). Finally, two slope species (*Argentina striata* and *Antennarius radiosus*) were present in the mid- and outer-shelf assemblages (Table 2, Appendix).

Cross-shelf patterns in juvenile fish assemblages and environmental variables

The juvenile fish assemblages and environmental variables all showed a cross-shelf gradient, which was correlated with depth during three of the four seasons (Table 6). The relationship between the other environmental variables and assemblages varied with season. In spring, the gradient in the inner- and mid-shelf and outer-shelf was mainly along the first dimension (Table 5) and was influenced by depth, bottom salinity, and bottom density (Fig. 5A). Inner- and mid-shelf stations were shallower and had less saline and dense bottom water than outer-shelf stations (Fig. 2). The spread along the second dimension in the outer-shelf group was less important (Table 5) and was influenced by the higher stratification of the outer stations (Fig. 2). A Monte Carlo permutation test of the environmental variables for spring indicated that depth, stratification, and bottom density were significantly related to the juvenile assemblages and the grouping of stations in the CCA (Table 6).

The summer juvenile assemblage was not related to these environmental variables. The ordination of the station and species data changed with the inclusion of environmental data to the analyses, indicating a poor relationship between the juvenile data and the environment (Fig. 5B) The low eigenvalues also indicated that very little of the observed variation in the data was explained by the environment (Table 5). These results agree with the results from the CA, both of which indicate that the entire shelf is a single assemblage.

The fall cross-shelf patterns in the juvenile fish assemblages were related to depth and bottom salinity (Fig. 5C). The first dimension had the highest eigenvalue and species-environment correlation (Table 5)

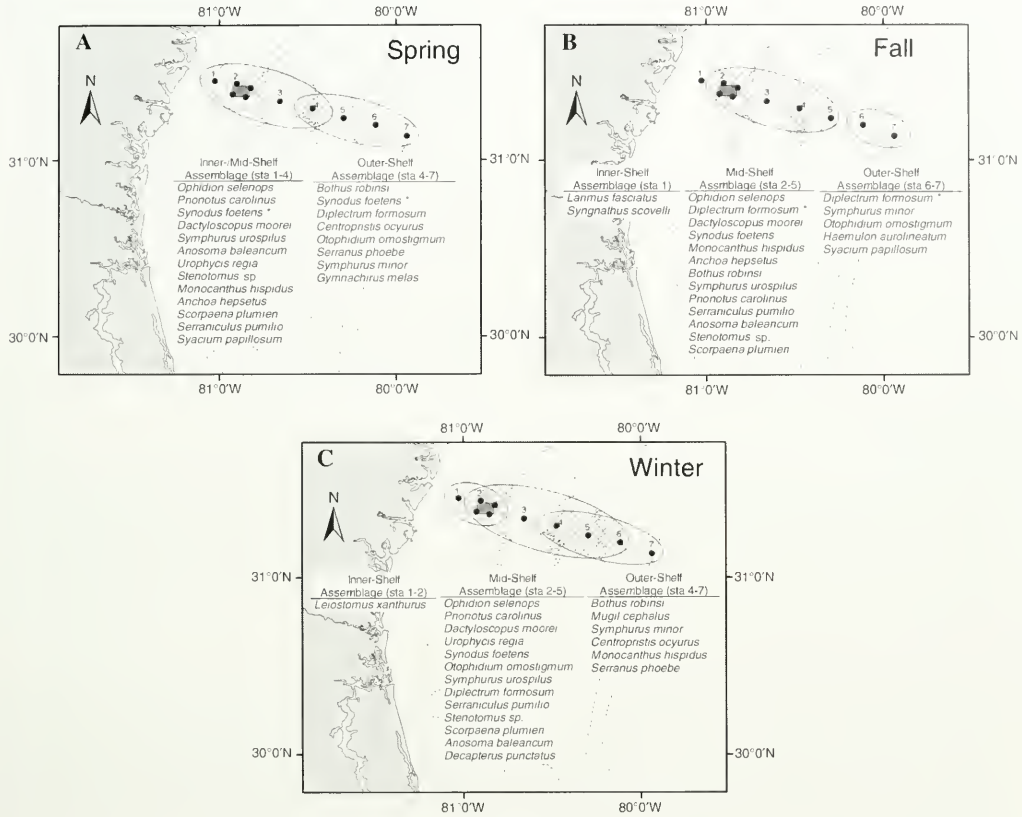

Figure 4

Cross-shelf juvenile fish assemblages identified from correspondence analysis for spring (**A**), fall (**B**), and winter (**C**). Summer was not plotted because there was only one summer assemblage. Hatched circles enclose stations that grouped together each season. Taxa from the 10% cross-shelf data set, in order of abundance, for each assemblage are shown in the tables. Asterisks indicate species that were found in multiple assemblages.

and was mainly influenced by depth; the shallower inner- and mid-shelf stations were separate from the outer-shelf stations. The second dimension was related to bottom salinity (Fig. 5C) and correlated with the separation of the inner-shelf station from the higher saline mid- and outer-shelf stations (Fig. 2). A Monte Carlo permutation test of the relationships between the assemblages and environmental data for the fall indicated that depth and bottom salinity were significantly related to the juvenile assemblages and cross-shelf station groups (Table 6).

The inclusion of environmental variables in the analysis of winter juvenile assemblage showed a weak relationship with the cross-shelf groups and juvenile assemblages, as indicated by the CCA correlation (Table 5). The addition of the environmental data also changed the ordination of the stations (Fig. 5D); yet there was still a cross-shelf gradient. Along the first dimension, depth, bottom temperature, and stratification were related to the juvenile assemblages and cross-shelf groups (Fig. 5D). The shallow inner- and mid-shelf groups were lower in bottom temperature and stratification, whereas bottom density was lowest on the inner- and outer-shelves and highest on the mid-shelf (Fig. 2). A Monte Carlo permutation test for the winter relationships indicated that depth and bottom density were significantly correlated with the fish assemblages and station groups (Table 6), although the bottom density did not appear to have any relation to the patterns described (Fig. 5D).

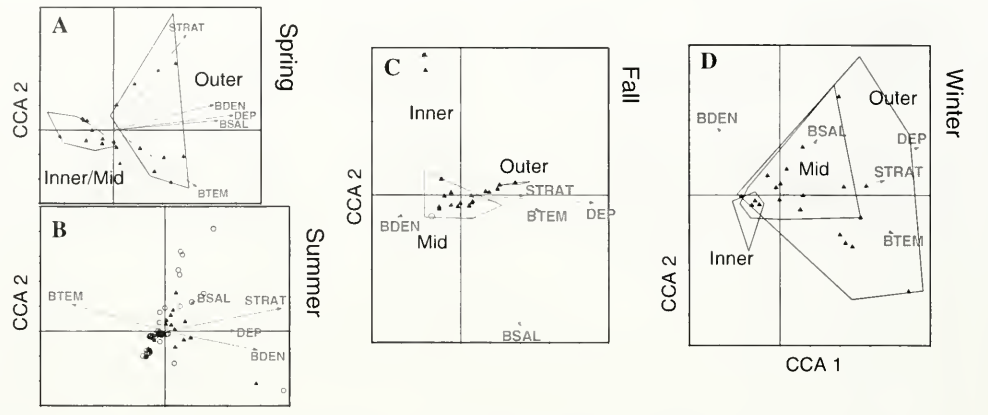

Figure 5

Canonical correspondence analysis ordinations (portraying the first and second dimension scores) of the 10% cross-shelf data set showing the correlations between environmental variables, species, and station groups each season; spring (**A**), summer (**B**), fall (**C**), and winter (**D**). The solid triangles mark the locations of taxa, and the polygons enclose the boundary of each station group with three or more stations (as in Fig. 3). If stations were not grouped, circles mark the locations. The arrows depict the gradient of each environmental variable (temperature=btemp, salinity=bsal, density=bden, stratification=strat, and depth=dep). The dashed lines intersect at the origin of the plot. Analyses were conducted by using both juvenile abundance and environmental data.

Seasonal patterns in juvenile fish assemblages

Many of the species (>68%) were present on the shelf in more than one season, which resulted in a large overlap of the seasonal assemblages (ordination not shown), including 12 of the 23 reef-associated species (Table 2). The assemblage data could be explained in three dimensions (as determined by CA of the 10% cross-shelf data set [Table 5]) and portrayed seasonal and cross-shelf patterns. Along the first dimension, there was separation between the winter inner-shelf assemblage and all other assemblages. The second and third dimensions portrayed a cross-shelf gradient in the spring, fall, and winter juvenile assemblage data. The summer assemblage overlapped all the cross-shelf groups from the other seasons except the winter inner-shelf assemblage. High abundances of *Larimus fasciatus* in the fall and *Leiostomus xanthurus* and *Mugil cephalus* in the winter (Table 2) caused these two seasons to be more dissimilar than were spring and summer, which were very similar. Many of the juveniles were found in the same cross-shelf assemblages during each season, whereas others shifted assemblages (Fig. 4).

Relation between seasonal juvenile assemblages and environmental variables

There appeared to be no relationship between the seasonal juvenile assemblages and environmental variables. The products of the CCA eigenvalues and species-environment correlations were extremely low (Table 5), and the CCA ordination of seasonal juvenile assemblages and environmental variables was different from the CA ordination. Thus, over the entire year, environmental variables did not help explain among-season variation in the juvenile assemblage data.

Along-shelf and cross-shelf patterns in the inshore juvenile fish data set

The inshore data set was made up of estuarine, coastal, and open-shelf species (Table 3, Appendix). There was a cross-shelf gradient in the spring and winter (Fig. 6). The innermost station group (8-m) separated from the other station groups along the first dimension (Fig. 7A) in spring. Most taxa from the 8-m assemblage (5 of 7) were not collected in high enough abundance to be included in the cross-shelf data set (Tables 2 and 3). In winter there was also a gradient from shallow to deeper stations (Fig. 6C). The assemblage nearest the origin in the winter (8-m assemblage) included estuarine species that were abundant at all the inshore stations (Table 3, Appendix). The coastal species, however, were more abundant at the deeper (12-m, 15-m, and 18-m) station groups (Table 3). There was no pattern in the along-shelf transects, from north to south, during either season (Fig. 6, B and D).

Along-shelf and cross-shelf patterns in the offshore juvenile fish data set

The offshore juvenile fish data set included primarily (76%) coastal, open-shelf, and slope species (Table 4, Appendix) and patterns in the data set varied with season. During the fall, there were both cross-shelf (Fig. 7A) and along-shelf patterns (Fig. 7B). Along the first dimension, there was a cross-shelf gradient (Fig. 7A) from the shallow stations (30–45 m depth; Fig. 1C) to the 50-m station group. The juvenile assemblage at the 50-m station group had high abundances of reef-associated species (Table 4). The stations on the northern most transect (Fig. 1C) also separated from the others along the second dimension, and had higher abundances of reef-associated species. The cross-shelf pattern was present in the winter, with greater abundances of reef-associated species at the 50-m station group (Fig. 7C), but there was no along-shelf pattern (Fig. 7D).

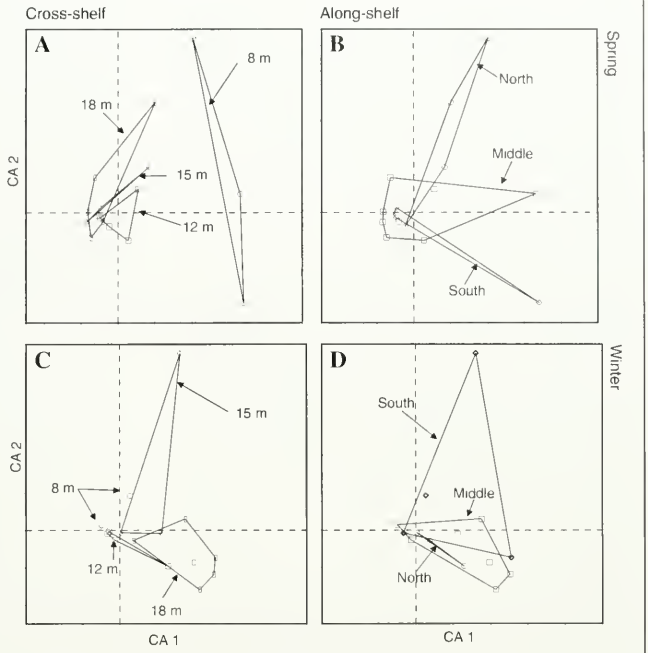

Figure 6

Correspondence analysis ordinations (portraying the first and second dimension scores) of the inshore juvenile fish community data showing cross-shelf and along-shelf station groups in spring (**A** and **B**) and winter (**C** and **D**). Solid lines enclose the boundary of each station group with three or more stations. Station groups comprising one or two stations are not enclosed by a solid line. Each station group is labeled and portrayed with a different symbol. The dashed lines intersect at the origin of the plot. Analyses were conducted by using juvenile fish abundance data only.

Discussion

One hundred and twenty-one taxa of juvenile fish were collected on unconsolidated sediments on the continental shelf off Georgia. The actual number of species was higher, but taxonomic problems limited species identification (e.g., identification of *Etropus* spp., *Prionotus* spp., *Sphoeroides* spp., and *Microgobius* spp.). With concurrent ichthyoplankton sampling of the cross-shelf stations (Fig. 1), we collected 161 taxa (Marancik et al., 2005); the larval community had more pelagic species, including several scombrids (e.g., *Auxis rochei*, *Scomberomorus cavalla*, and *S. maculatus*) and 17 myctophids. The large juvenile and adult fish communities of the shallow coastal zone (<10 m) and continental shelf (9–180 m) comprised about 150 species, including both pelagic and demersal species (Wenner et al.[4,5,6,7]; Wenner and Sedberry, 1989). A maximum of 164 species were reported from rocky-reefs in the region (Chester et al., 1984; Parker et al. 1994; Baron et al., 2004). Fewer species inhabit estuaries than shelf habitats of the southeast (<90), particularly

[4] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979a. Results of MARMAP otter trawl investigations in the South Atlantic Bight. II, spring 1974, 78 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

[5] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979b. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III, summer 1974, 62 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

[6] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979c. Results of MARMAP otter trawl investigations in the South Atlantic Bight. IV, winter-early spring 1975, 59 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

[7] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1980. Results of MARMAP otter trawl investigations in the South Atlantic Bight. V, summer 1975, 57 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

if different habitat types are considered (Ross and Epperly, 1985; Hettler, 1989; Nelson et al., 1991). Thus, unconsolidated sediments are as rich a habitat in terms of the number of species, as are pelagic, rocky reef, and estuarine habitats in the southeast U.S. continental shelf ecosystem.

Cross-shelf regions were defined on the Georgia shelf from spatial patterns in juvenile fish distributions. The number and extent of cross-shelf regions varied seasonally, but in general, three regions were identified: inner-shelf, mid-shelf, and outer-shelf regions. Juvenile assemblages were associated with the regions, yet some individual species were distributed across regions. Juveniles of year-round residents (e.g., *Ophidion selenops*, *Diplectrum formosum*, and *Prionotus carolinus*) were usually the most abundant species, although transient juveniles (e.g., *Leiostomus xanthurus*, *Lagodon rhomboides*, and *Brevoortia tyrannus*) were seasonally abundant. Cross-shelf gradients in species distribution have been found for other organisms and life stages of fish on the southeast U.S. shelf (macroinfauna: Atkinson et al., 1985; larval fish: Marancik et al., 2005; adult reef fish: Chester et al., 1984; adult demersal fish: Wenner et al.[4,5,6,7]). Cross-shelf gradients also are common in demersal juvenile fish distributions in other continental shelf ecosystems (northwest U.S.: Norcross et al., 1997; Toole et al., 1997; Abookire and Norcross, 1998; Bailey et al., 2003; Johnson et al., 2003; northeast U.S.: Steves et al., 2000; Sullivan et al., 2000; southwest U.S.: Johnson et al., 2001).

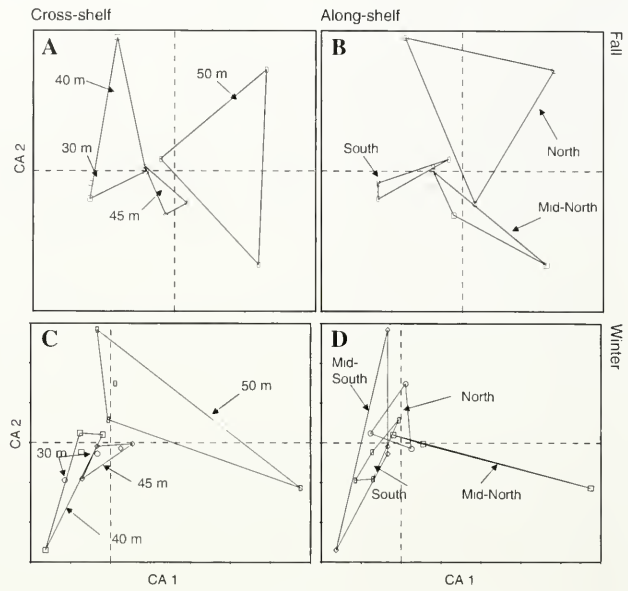

Figure 7

Correspondence analysis ordinations (portraying the first and second dimension scores) of the offshore juvenile fish community data showing cross-shelf and along-shelf station groups in fall (**A** and **B**) and winter (**C** and **D**). Solid lines enclose the boundary of each station group with three or more stations. Station groups comprising one or two stations are not enclosed by a solid line. Each station group is labeled and portrayed with a different symbol. The dashed lines intersect at the origin of the plot. Analyses were conducted by using juvenile fish abundance data only.

The cause of cross-shelf gradients in juvenile fish distribution is difficult to determine. The primary environmental variable correlated with cross-shelf juvenile fish assemblages is often depth (Table 6; Norcross et al., 1997; Steves et al., 2000; Sullivan et al., 2000; Johnson et al., 2001; Johnson et al., 2003), although temperature, salinity, and sediment grain size also are correlated with depth (Norcross et al., 1997; Steves et al., 2000; Sullivan et al., 2000). On the Georgia shelf, salinity, density, and stratification correlated with the distribution of juvenile assemblages during the spring, fall, and winter (Table 6), and along with temperature (Figs. 2 and 6) likely influenced the distribution of juvenile fish, but the causative mechanisms remain unresolved. On the northeast U.S. shelf, cold bottom water left from winter resides on the mid-shelf during summer and fall (cold pool; Ketchum and Corwin, 1964). Steves et al. (2000) and Sullivan et al. (2000) hypothesized that cross-shelf patterns in settlement and juvenile fish distributions were caused by cross-shelf temperature gradients related to the presence of the cold pool on the mid-shelf. Similarly, juvenile flatfish species in Alaska exhibited cross-shelf gradients in habitat use that were influenced by temperature-depth interactions (Norcross et al., 1997). *Hippoglossoides elassodon* were most abundant in the colder, deeper locations, and *Hippoglossus stenolepis* were more abundant in the warmer, shallow locations (Norcross et al., 1997). On the Georgia shelf, juvenile assemblages were less distinct during summer, when environmental gradients were weakest, providing some support for the hypothesis that cross-shelf patterns in juvenile distribution were caused by environmental factors. Alternatively, in other studies it has been hypothesized that juvenile distribution results from selection of specific habitat characteristics within large-scale environmental gradients (Stoner and Abookire, 2002). For example, laboratory and field

studies have found that some fish species select specific sediment characteristics or biogenic structures (Stoner and Abookire, 2002; Diaz et al., 2003; Stoner and Titgen, 2003), and spatial patterns in these habitat characteristics may cause spatial patterns in juvenile fish distribution. We did not stratify sampling by sediment characteristics or biogenic structures and thus we could draw no conclusion regarding the role of habitat characteristics in influencing juvenile fish distribution on the Georgia shelf.

No along-shelf spatial patterns were found in the juvenile fish community on the continental shelf off the Georgia coast; however, the along-shelf dimension sampled (~60 km) was relatively small compared to the along-shelf dimension of the southeast U.S. continental shelf ecosystem (~1000 km). Consistent patterns in along-shelf gradients in oceanographic features (Atkinson et al., 1985; Lee et al., 1991) and adult fish communities (Chester et al., 1984; Wenner and Sedberry, 1989) exist on the southeast U.S. shelf, but over larger along-shelf dimensions than sampled in the present study (200–400 km). Consistent patterns of juvenile use of along-shelf habitat over smaller dimensions (~100 km) have been reported for other shelf ecosystems (northwest U.S.: Norcross et al., 1997; Abookire and Norcross, 1998; northeast U.S.: Steves et al., 2000; Sullivan et al., 2000), but the relation to along-shelf environmental and habitat characteristics is unclear. Along-shelf patterns in juvenile fish distribution on unconsolidated sediments may occur on the southeast U.S. shelf, but at dimensions larger than 60–100 km.

Seasonal patterns in settlement and postsettlement movement both defined and blurred classification of juvenile fish assemblages on the Georgia shelf. Many of the resident shelf species were consistently collected in the same cross-shelf regions (i.e., inner and mid-shelf: *Ophidion selenops, Prionotus carolinus, Dactyloscopus moorei, Stenotomus* sp., and *Serraniculus pumilio*; outer-shelf: *Symphurus minor, Serranus phoebe, Centropristis ocyurus,* and *Bothus lunatus*), and the consistent collection of these species helped form a definition of juvenile assemblages. Other resident species shifted juvenile assemblages (e.g., *Diplectrum formosum, Monacanthus hispidus, Bothus robinsi, Otophidium omostigmum*, and *Bothus ocellatus*), possibly because of seasonal changes in settlement patterns or ontogenetic postsettlement movements, with the result that some classifications were blurred. Four scieanid species, present during the spring, summer, and fall as larvae (Marancik et al., 2005), were collected during the fall as juveniles and contributed to defining the fall inner-shelf (*Larimus fasciatus* and *Menticirrhus americanus*) and mid-shelf (*Cynosion nothus* and *C. regalis*) juvenile assemblages. These species may shift settlement or juvenile habitat (or both) between estuaries and the coastal ocean; this shift has been shown to occur off the coast of New Jersey (Able et al., 2003; Neuman and Able, 2003). Further, a number of species in the ecosystem spawn on the shelf yet use estuarine habitats as juvenile nurseries (Warlen and Burke, 1990; Able and Fahay, 1998). In our study, settlement stage *L. xanthurus, Brevoortia tyrannus*, and *Lagodon rhomboides* were collected on the shelf, and contributed to the definition of the inner- and mid-shelf assemblages. Some individuals of these estuarine-dependent species may not settle directly into estuarine habitats as has been demonstrated for *Centropristis striata* off the coast of New Jersey (Able and Fahay, 1998).

Only a few reef-associated species collected during the study used unconsolidated sediments consistently. *Centropristis ocyurus, Diplectrum formosum*, and *Stenotomus* sp. were the most common reef fishes collected on unconsolidated sediments, and made up >1% of the total catch (Appendix). Other less frequently occurring juveniles of important reef-associated species that were collected were *Centropristis striata, Epinephelus niveatus, Pristigenys alta, Priacanthus arenatus*, and *Lutjanus analis*.

Reef-associated species were collected across the entire shelf. *Centropristis ocyurus* and *Stenotomus* sp. were commonly collected on the outer-, inner-, and mid-shelves, respectively (Table 2, Appendix). *Centropristis striata*, which uses habitats in estuaries and coastal regions as juveniles (Able and Fahay, 1998), was collected on the inner- and mid-shelf in the spring and summer, during periods of high settlement (Able and Hales, 1997). The presence of many reef-associated species at the deeper (50 m) stations (Table 4) may indicate greater use of offshore unconsolidated sediments by reef-associated species or that sampling was done in an area closer to rocky-reefs. Several species of the South Atlantic Fishery Management Council snapper-grouper complex have been reported to use a variety of nonreef habitats as newly settled juveniles, including unconsolidated sediments on the shelf (Lindeman et al., 2000). Many coral reef fish also use several types of nearshore nonreef habitat as juveniles (de la Moriniere et al., 2002; Nagelkerken and van der Velde, 2002). These nonreef habitats are assumed to be important nursery habitats; however, strong evidence of movement from juvenile to adult habitats has been documented only for a few reef-associated fishes (Gillanders et al., 2003). The fact that reef-associated species also use unconsolidated sediments indicates there is an interdependence between reef habitats and unconsolidated sediments; yet the function of each habitat remains unquantified.

In addition to reef species, a number of commercially and recreationally important demersal species used unconsolidated sediments on the shelf off Georgia as juvenile habitat. Juvenile *Cynoscion nothus, C. regalis* and *Menticirrhus americanus* were collected on the inner- and mid-shelves in the fall, and settlement-size *Leiostomus xanthurus* were collected in the winter. However, small noncommercial demersal species were the most abundant juveniles collected during beam trawl sampling.

Much of the southeast U.S. continental shelf is impacted by trawl fisheries that can adversely impact unconsolidated sediments (Barnette[3]). Current manage-

ment concerns focus primarily on bycatch reduction, impacts on stock assessments of commercially and recreationally important finfish, and destruction of coral, live hard-bottom, and SAV habitat (NOAA[8]; Barnette[3]). The presence of reef-associated and sciaenid species in our samples indicate that the unconsolidated sediments of the shelf are potentially important habitats for early life stages, and that trawl fisheries on the shelf may impact the population dynamics of these species. Equally important may be the ecological effects on the small noncommercial demersal species that dominate the catch on unconsolidated sediments and that are abundant in the shrimp trawl bycatch (SAFMC, 1996).

Unconsolidated sediments serve as juvenile habitat for a number of species in the southeast U.S. shelf ecosystem. Some species use unconsolidated sediments throughout their life history, but for a number of species, unconsolidated sediments serve as only one of a mosaic of habitats through the life history (see Browman and Konstantinos, 2004). Additionally, there is growing recognition of the importance of unconsolidated sediments in the trophic ecology of the southeast U.S. shelf. Benthic primary production of the shelf has been shown to be 4–6 times greater than water-column production at specific locations (Nelson et al., 1999). Unconsolidated sediments are areas of reef fish feeding (Sedberry, 1985, 1990) and several important fish predators inhabit unconsolidated sediments (triglids, synodontids, Ross, 1976; Richards et al., 1979). Current ecosystem approaches to fisheries (see Sissenwine and Murawski, 2004) in the region largely ignore unconsolidated sediments (SAFMC, 1998, 2001), and although the importance of this habitat to juvenile fish production remains unquantified (sensu Beck et al., 2001), management efforts would be improved through a greater recognition of the potential importance of these habitats to fisheries production and the interconnectedness of multiple habitats in the southeast U.S. continental shelf ecosystem.

Acknowledgments

We would like to thank all who helped with sample collections, sorting, and analyses: G. Bohne, R. Bohne, C. Bonn, J. Burke, M. Burton, B. Degan, M. Duncan, J. Govoni, M. Greene, E. Jugovich, S. Lem, J. Loefer, R. Mays, G. McFall, R. McNatt, A. Powell, R. Rogers, S. Shoffler, S. Varnam, and T. Zimanski. We would like to thank NOAA's Undersea Research Center at the University of North Carolina at Wilmington for use of the ROV and L. Horn for operating the ROV. We appreciate the hard work and dedication of the officers and crew of the NOAA Ship *Ferrel*, NOAA Ship *Jane Yarn*, NOAA Ship *Oregon* II, and RV *Cape Fear*. We would also like to thank A. Powell, M. Sullivan, J. Merriner, and an anonymous reviewer for their comments on previous drafts. Gray's Reef National Marine Sanctuary, the National Marine Sanctuary Office, and Center for Coastal Fisheries and Habitat Research provided funding for the project.

[8] NOAA (National Oceanic and Atmospheric Administration). 1998. Managing the nation's bycatch: priorities, programs, and actions for the National Marine Fisheries Service, 199 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

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Appendix

Juvenile taxa collected in beam trawl collections from the continental shelf off the coast of Georgia, USA. Seasonal catch per unit of effort (CPUE, fish/5 min) was calculated from cross-shelf stations (see Fig. 1 and Table 1). Mean (SD) of the total CPUE and standard length (SL, mm) was calculated from all stations. Adult distributions (AD) and whether species are reef-associated (RA) was determined from the literature. E = estuarine, C = coastal (0–20 m), O = open-shelf (20–70 m), Sl = slope (>70 m), W = weakly reef-associated, and S = strongly reef-associated.

		Cross-shelf stations				All stations			
		Mean				CPUE	SL (mm)		
Family	Species	Spring	Summer	Fall	Winter	Mean (SD)	Mean (SD)	AD	RA
Elopidae	*Elops saurus*		0.02		0.01	0.007 (±0.084)	46.7 (±15.9)	E, C	
Muraenidae	*Gymnothorax saxicola*					0.005 (±0.069)	69.5 (±0.7)	C, O	
Ophichthidae	*Ophichthus gomesii*		0.01			0.009 (±0.119)	103.3 (±20.1)	E, C, O	
	Ophichthus ocellatus	0.05		0.03	0.02	0.016 (±0.133)	160.9 (±59.2)	E, C, O	
Congridae	*Ariosoma balearicum*	0.39	0.10	0.30	0.02	0.135 (±0.431)	126.5 (±44.2)	E, C, O	
Clupeidae	*Brevoortia tyrannus*				0.07	0.014 (±0.116)	24.5 (±1.8)	E, C, O	
	Etrumeus teres	0.02			0.01	0.005 (±0.069)	31.8 (±1.1)	C, O	
	Sardinella aurita		0.01			0.005 (±0.069)	36.0 (±2.8)	C, O	
Engraulididae	*Anchoa hepsetus*	0.09	0.19	1.14		0.355 (±2.631)	31.3 (±10.2)	E, C, O	
	Anchoa lamprotaena			0.07		0.015 (±0.215)	44.5 (±5.8)	C	
Argentinidae	*Argentina striata*				0.02	0.005 (±0.069)	52.0 (±1.4)	Sl	
Synodontidae	*Synodus foetens*	1.00	0.45	1.55	0.39	0.643 (±1.570)	65.8 (±40.1)	E, C, O	
	Synodus poeyi	0.26				0.035 (±0.420)	33.1 (±3.5)	O	
	Trachinocephalus myops	0.13	0.06	0.22	0.06	0.091 (±0.354)	92.3 (±47.6)	O	
Gadidae	*Urophycis regia*	0.28			0.68	0.302 (±0.867)	69.7 (±21.3)	C, O	
Ophidiidae	*Ophidion grayi*	0.02				0.002 (±0.049)	39.0	C, O	
	Ophidion holbrooki	0.70				0.121 (±1.226)	98.8 (±47.3)	C, O	
	Ophidion marginatum	0.11	0.03	0.01	0.03	0.050 (±0.270)	94.8 (±43.0)	C, O	
	Ophidion selenops	3.63	0.35	4.92	1.49	1.823 (±4.373)	56.1 (±19.7)	O	
	Ophidion welshi	0.12		0.02		0.019 (±0.194)	107.9 (±27.1)	C, O	
	Otophidium omostigmum	0.60	0.09	0.69	0.38	0.392 (±1.192)	60.0 (±21.8)	O	
Batrachoididae	*Porichtys plectrodon*			0.03		0.007 (±0.078)	56.3 (±13.7)	C, O	
Antennariidae	*Antennarius ocellatus*					0.002 (±0.048)	47.0	O, Sl	W
	Antennarius radiosus				0.02	0.010 (±0.102)	24.0 (±4.1)	O, Sl	W
Ogcocephalidae	*Halieutichthys aculeatus*	0.02	0.04			0.014 (±0.118)	14.4 (±1.5)	C, O	
	Ogcocephalus nasutus	0.02	0.05		0.01	0.025 (±0.154)	29.0 (±17.8)	C, O	
	Ogcocephalus parvus				0.02	0.012 (±0.108)	75.6 (±34.1)	O	

continued

Appendix (continued)

		Cross-shelf stations				All stations			
		Mean				CPUE	SL (mm)		
Family	Species	Spring	Summer	Fall	Winter	Mean (SD)	Mean (SD)	AD	RA
Exocetidae	*Hemiramphus balao*			0.02		0.003 (±0.052)	80.0	C, O	
	Hemiramphus brasiliensis		0.01			0.002 (±0.049)	97.0	C, O	
	Hirundichthys affinis		0.05	0.02		0.017 (±0.146)	35.4 (±13.8)	C, O	
	Parexocoetus brachypterus			0.02		0.002 (±0.048)	34.0	O	
Syngnathidae	*Hippocampus erectus*	0.12	0.04	0.01	0.04	0.055 (±0.236)	60.8 (±19.9)	E, C	
	Syngnathus scovelli		0.06	0.02		0.019 (±0.166)	56.3 (±11.8)	E, C	
	Syngnathus springeri	0.02	0.01		0.07	0.021 (±0.144)	64.3 (±6.9)	C, O	
Scorpaenidae	*Scorpaena dispar*		0.02	0.07		0.043 (±0.458)	39.4 (±21.6)	C, O	W
	Scorpaena plumieri	0.07	0.13	0.08	0.02	0.078 (±0.335)	43.5 (±31.0)	C, O	W
Triglidae	*Prionotus* spp.	0.73	0.17	15.31	0.52	2.700 (±9.684)	11.6 (±3.3)	C, O	
	Bellator brachychir		0.01	0.01		0.007 (±0.079)	27.0 (±13.2)	O	
	Bellator militaris	0.01	0.01			0.004 (±0.063)	17.5 (±12.0)	O	
	Prionotus carolinus	3.04	0.32	0.42	1.08	1.127 (±2.801)	53.5 (±27.9)	E, C, O	
	Prionotus evolans	0.03				0.004 (±0.081)	90.0 (±62.2)	E, C, O	
	Prionotus ophryas		0.01			0.002 (±0.049)	16.0	C, O	
	Prionotus scitulus				0.08	0.033 (±0.180)	133.3 (±19.4)	C, O	
Serranidae	*Centropristis ocyurus*	0.73	0.04		0.08	0.313 (±1.592)	31.0 (±12.0)	O	W
	Centropristis striata	0.07	0.04			0.017 (±0.161)	33.1 (±14.8)	E, C, O	S
	Diplectrum formosum	0.96	2.50	2.39	0.16	1.360 (±3.378)	28.2 (±23.8)	C, O	W
	Epinephelus niveatus					0.005 (±0.069)	29.0 (±7.1)	Sl	S
	Serraniculus pumilio	0.03	0.21	0.34	0.12	0.155 (±0.734)	22.5 (±7.5)	C, O	W
	Serranus phoebe	0.31	0.04	0.02	0.04	0.220 (±1.618)	21.6 (18.1)	C, O	W
	Serranus subligarius					0.007 (±0.146)	30.7 (±9.3)	C, O	S
Grammistidae	*Rypticus* spp.			0.01		0.046 (±0.590)	41.8 (±12.9)	C, O	S
	Rypticus bistrispinus					0.054 (±0.596)	42.5 (±5.2)	C, O	S
Priacanthidae	*Priacanthus arenatus*		0.01			0.002 (±0.049)	15.0	O	S
	Pristigenys alta		0.02	0.05		0.016 (±0.126)	17.7 (±8.6)	O	S
Apogonidae	*Apogon* sp.	0.01	0.03			0.011 (±0.125)	20.9 (±11.0)	O	W
	Astrapogon spp./*Epigonus* spp.		0.01			0.002 (±0.049)	9.2		
	Apogon maculatus					0.061 (±0.680)	17.6 (±3.5)	O	W
	Apogon pseudomaculatus		0.04			0.028 (±0.213)	18.6 (±14.1)	O	W
Carangidae	Carangidae				0.02	0.005 (±0.068)	18.5 (±6.4)		
	Decapterus spp.		0.14			0.031 (±0.278)	24.8 (±5.7)	O	
	Caranx bartholomaei	0.02				0.002 (±0.044)	12.0	C, O	
	Caranx crysos			0.02		0.002 (±0.049)	101.0	C, O	W
	Chloroscombrus chrysurus		0.01	0.06		0.010 (±0.107)	15.1 (±3.6)	C, O	W
	Decapterus macarellus	0.02			0.01	0.005 (±0.069)	23.0 (±4.2)	O	
	Decapterus punctatus		0.05	0.01		0.017 (±0.188)	27.6 (±5.8)	C, O	
	Trachurus lathami	0.02				0.002 (±0.046)	16.0	C, O	
Lutjanidae	*Lutjanus analis*		0.01			0.002 (±0.049)	18.0	C, O	S
Haemulidae	*Haemulon aurolineatum*		0.05	0.05		0.016 (±0.185)	45.3 (±26.8)	C, O	W
Sparidae	*Stenotomus* sp.	0.18	0.16	0.14	0.08	0.135 (±0.823)	46.1 (±28.4)	C, O	W
	Lagodon rhomboides				0.06	0.012 (±0.128)	27.1 (±27.9)	E, C, O	W
Sciaenidae	*Cynoscion nothus*		0.04			0.006 (±0.095)	9.8 (±0.9)	E, C	
	Cynoscion regalis		0.06			0.008 (±0.102)	10.3 (±0.8)	E, C	
	Larimus fasciatus		0.19			0.027 (±0.313)	14.7 (±4.7)	E, C	
	Leiostomus xanthurus			2.27		3.361 (22.193)	16.2 (±1.7)	E, C, O	

continued

Appendix (continued)

		Cross-shelf stations				All stations			
		Mean				CPUE	SL (mm)		
Family	Species	Spring	Summer	Fall	Winter	Mean (SD)	Mean (SD)	AD	RA
Sciaenidae (cont.)	*Menticirrhus americanus*		0.07			0.010 (±0.159)	13.3 (±9.1)	E, C	
	Stellifer laceolatus					0.005 (±0.097)	75.0 (±0.0)	E, C	
Mullidae	*Upeneus parvus*					0.002 (±0.049)	48.0	C, O	
Mugilidae	*Mugil cepholus*				0.18	0.047 (±0.422)	21.7 (±2.3)	E, C, O	
	Mugil curema		0.01		0.02	0.027 (±0.214)	21.8 (±1.5)	E, C, O	
Labridae	*Halichoeres bivittatus*		0.02			0.010 (±0.152)	71.0 (±5.0)	O	S
	Xyrichtys novacula		0.01			0.002 (±0.049)	41.5	O	
Scaridae	Scaridae		0.03			0.009 (±0.093)	41.3 (±31.8)		
Uranoscopidae	*Kathetostoma albigutta*				0.01	0.002 (±0.049)	26.0	O	
Dactyloscopidae	*Dactyloscopus moorei*	0.80	0.17	2.09	0.80	0.689 (±2.073)	22.1 (±5.1)	O	
Blenniidae	*Chasmodes/Parablennius marmoreus*		0.04			0.007 (±0.109)	19.0 (±2.6)	E, C	S
	Hypleurochilus geminatus	0.04	0.01			0.021 (±0.160)	43.6 (±17.2)	E, C	
	Parablennius marmoreus		0.02			0.009 (±0.119)	20.3 (±4.3)	E, C	S
Callionymidae	*Diplogrammus pauciradiatus*		0.07			0.025 (±0.170)	9.5 (±1.0)	O	
Gobiidae	*Microgobius* spp.	0.06	0.82	1.42	0.01	0.454 (±1.424)	16.7 (±1.9)		
	Gobiosoma bosci				0.01	0.014 (±0.150)	19.5 (±1.5)	E, C	
	Gobiosoma ginsburgi				0.02	0.005 (±0.068)	22.5 (±3.5)	E, C	W
	Ioglossus calliurus	0.01				0.002 (±0.041)	14.7	C, O	
Stromateidae	*Peprilus triacanthus*	0.07	0.01		0.08	0.042 (±0.250)	25.3 (±11.7)	C, O	
Bothidae	*Bothus ocellatus/robinsi*	0.07	0.08	0.07		0.041 (±0.254)	15.9 (±2.6)		
	Bothus spp.	0.86	0.41	4.50	0.33	0.971 (±3.728)	18.4 (±3.0)	O	
	Bothus lunatus	0.02			0.01	0.005 (±0.069)	79.0 (±9.9)	E, C, O	
	Bothus ocellatus		0.03	0.04	0.01	0.046 (±0.341)	33.4 (±23.5)	C, O	
	Bothus robinsi	1.21	0.23	0.52	0.34	0.435 (±1.464)	37.3 (±35.7)	C, O	
Paralichthyidae	*Citharichthys* spp.	0.19	0.03		0.41	0.132 (±0.671)	13.7 (±6.0)		
	Etropus spp.	8.89	1.31	2.96	15.97	10.563 (20.936)	18.3 (±8.2)		
	Ancylopsetta quadrocellata				0.22	0.114 (±0.386)	38.1 (±17.7)	C, O	
	Citharichthys gymnorhinus	0.03				0.004 (±0.063)	18.5 (±7.8)	O	
	Citharichthys macrops	0.20	0.04	0.02	0.13	0.090 (±0.441)	76.9 (±44.8)	C, O	
	Cyclopsetta fimbriata	0.03	0.04	0.05		0.037 (±0.226)	28.9 (±14.5)	O	
	Syacium papillosum	0.02	0.09	0.04		0.040 (±0.269)	16.5 (±17.2)	C, O	
Scopthalmidae	*Scopthalmus aquosus*				0.01	0.002 (±0.049)	14.0	E, C, O	
Soleidae	*Gymnachirus melas*	0.04	0.03			0.014 (±0.115)	17.1 (±7.5)	O	
Cynoglossidae	*Symphurus* spp.		0.01	0.02		0.005 (±0.067)	18.0 (±9.9)		
	Symphurus diomedeanus	0.05				0.007 (±0.109)	22.5 (±17.7)	O	
	Symphurus minor	0.26	0.25	1.87	0.15	0.552 (±1.878)	23.8 (±4.2)	O	
	Symphurus parvus	0.05	0.02			0.012 (±0.108)	15.9 (±1.7)	O	
	Symphurus plagiusa		0.02			0.029 (±0.270)	59.9 (±16.5)	E, C, O	
	Symphurus urospilus	0.42	0.24	0.43	0.28	0.257 (±0.717)	55.5 (±20.8)	O	
Balistidae	*Aluterus schoepfi*		0.01	0.02		0.005 (±0.066)	18.0 (±11.3)	C, O	W
	Cantherhines pullus					0.012 (±0.128)	18.5 (±1.5)	S	
	Monacanthus ciliatus	0.02				0.005 (±0.069)	41.0 (±26.9)		
	Monacanthus hispidus	0.18	0.54	1.36	0.06	0.460 (±1.314)	34.4 (±22.6)	C, O	
	Monacanthus setifer			0.01		0.004 (±0.063)	91.0 (±0.0)	O	
Ostraciidae	*Lactophyrs quadricornis*		0.01			0.009 (±0.090)	67.8 (±83.6)	O	W
Tetraodontidae	*Sphoeroides* spp.	0.03	0.13		0.01	0.126 (±0.600)	15.9 (±4.0)		
Diodontidae	*Chilomycterus schoepfi*	0.02				0.002 (±0.049)	17.0	E, C	

Growth and maturity of salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific, and comments on back-calculation methods

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Abstract—Age and growth estimates for salmon sharks (*Lamna ditropis*) in the eastern North Pacific were derived from 182 vertebral centra collected from sharks ranging in length from 62.2 to 213.4 cm precaudal length (PCL) and compared to previously published age and growth data for salmon sharks in the western North Pacific. Eastern North Pacific female and male salmon sharks were aged up to 20 and 17 years, respectively. Relative marginal increment (RMI) analysis showed that postnatal rings form annually between January and March. Von Bertalanffy growth parameters derived from vertebral length-at-age data are L_∞=207.4 cm PCL, k=0.17/yr, and t_0=−2.3 years for females (n=166), and L_∞=182.8 cm PCL, k=0.23/yr , and t_0=−1.9 years for males (n=16). Age at maturity was estimated to range from six to nine years for females (median precaudal length of 164.7 cm PCL) and from three to five years old for males (median precaudal length of 124.0 cm PCL). Weight-length relationships for females and males in the eastern North Pacific are $W=8.2\times10^{-05}\times L^{2.759}$ (r^2=0.99) and $W=3.2\times10^{-06}\times L^{3.383}$ (r^2=0.99), respectively. Our results show that female and male salmon sharks in the eastern North Pacific possess a faster growth rate, reach sexual maturity earlier, and attain greater weight-at-length than their same-sex counterparts living in the western North Pacific.

Manuscript submitted 23 October 2003 to the Scientific Editor's Office.

Manuscript approved for publication 15 September 2005 by the Scientific Editor.

Fish. Bull. 104:278–292 (2006).

The salmon shark (*Lamna ditropis*) is a large apex predator inhabiting the coastal and oceanic waters of the North Pacific Ocean, most commonly ranging from 65°N latitude to 35°N in the west and to 30°N in the east (Strasburg, 1958; Neave and Hanavan, 1960; Compagno, 1984, 2001; Blagoderov, 1994; Nagasawa, 1998). It is found individually and in large aggregations at sea-surface temperatures of 5°C to 18°C and has a depth distribution ranging from the surface to at least 150 m (Compagno, 1984, 2001). The salmon shark is a highly opportunistic predator, feeding on a wide variety of prey and sharing the highest trophic level of the food web in boreal and temperate North Pacific waters with marine mammals and seabirds (Brodeur, 1988; Nagasawa, 1998). Adult salmon sharks typically range in size from 180–210 cm precaudal length (PCL; = 200–260 cm total length, TL) and can weigh up to 220 kg (Tanaka, 1980; JAMARC, 1980; Nagasawa, 1998). Reported lengths of 300 cm TL and greater and weights exceeding 450 kg are unsubstantiated.

Salmon sharks are migratory in nature. North-south migrations have been documented on both sides of the North Pacific; northern movements occur in spring and southern movements are occur in autumn (Iino, 1939; Kosugi and Tsuchisaki, 1950; Gorbatenko and Cheblukova, 1990; Balgaderov, 1994; Nakano and Nagasawa, 1994). However, this species is present in boreal waters throughout the year (Goldman and Human, in press; Weng et al., 2005). Salmon sharks tagged with satellite transmitters have shown an extremely wide range of movements throughout the eastern North Pacific—movement as far south as southern California and Hawaii (Weng et al., 2005). To date, however, no salmon shark has been recorded moving across the Pacific, but such movements are suspected to occur (Nakano and Nagasawa 1996; Goldman and Musick, in press; Weng et al., 2005)

Sexual segregation is relatively common in sharks; however an extremely large sex ratio difference exists in salmon sharks across the North Pacific basin (Sano, 1962; Nagasawa, 1998; Goldman and Musick, in press). The western North Pacific (WNP) is male dominated and the eastern North Pacific (ENP) is female dominated. Male dominance in the WNP and female dominance in the ENP increase with increasing latitude. Larger sharks range farther north than smaller individuals, and

southern catches generally occur in deeper waters (Nagasawa, 1998; Goldman and Musick[1]).

Shark catches in Alaska waters have been reported to be as high as those from Washington, Oregon and California combined (Camhi, 1999), and there is concern over the amount of shark bycatch being taken (Gaichas[2]). In 1997, state managers closed commercial shark fishing in Alaska state waters and imposed conservative sport-fishing limits (1 shark per person per day, 2 per year) that legally encompass federal waters too. Federal managers are currently addressing elasmobranch management issues (Goldman, 2001).

Because of the ever-increasing importance of providing accurate and timely life history parameters to foster responsible management efforts, we had two main objectives in our study. The first was to estimate growth parameters and the age and length at sexual maturity of salmon sharks in the ENP. The second was to compare our results to those previously published on salmon sharks from the WNP to elucidate any existing variability in the life history parameters of this highly sexually segregated population. Lastly, because of the small number of samples for female juvenile age classes, a small overall sample size for males, and the fact that samples (for both sexes) were not obtained for each month, we applied several back-calculation methods to our data (see Cailliet and Goldman, 2004 and Goldman, 2004) and provide a demonstration and brief discussion on the importance of choosing an appropriate back-calculation method.

Materials and methods

Salmon shark vertebrae were obtained from numerous sources and locations ranging geographically from southern California to Kodiak Island (n=182) between 1997 and 2002. The majority of samples came from research cruises in the Gulf of Alaska (GOA) and Prince William Sound (PWS), by accompanying sport-fishing vessels on salmon shark trips in the GOA and PWS, and from Alaska Department of Fish and Game (ADF&G) port samplers. Vertebral samples collected from British Columbia to southern California came from incidental catches and recently beached animals.

Precaudal, fork, and total length (PCL, FL, and TL) were measured on a straight line and recorded along with date, location, and sex (and clasper length in males). Samples provided by additional sources included at least one of the necessary straight-line measurements, date and location of capture or wash-up, and sex. Weights were obtained from 20 females ranging from 67.1 to 213.4 cm PCL, and 7 males ranging from 69.5 to 187 cm PCL. The power function, $W = aL^b$, was fitted to the data (in SigmaPlot, vers. 6.0, SPSS Inc., Chicago, IL), where W = weight (kg) and L = length (cm PCL). Specimens weighed had been collected from southern California to Alaska. A likelihood ratio test was used to determine whether differences between female and male weight-length parameters were significant or if a single set of parameters described the data better (Kimura, 1980; Quinn and Deriso, 1999; Haddon, 2001) (SAS, vers. 8.0, SAS, Cary, NC). A 20- to 25-cm section of vertebrae was removed from directly in front of the first dorsal fin (above the gills) and stored frozen. We used PCL measurements to make direct comparisons with previously published salmon shark age and growth data from the WNP. Linear regression equations, based on our samples, were developed for converting PCL to FL and TL.

Vertebral samples were thawed, cleaned of excess tissue, separated into individual centra and stored in 70% ethyl alcohol for at least 24 h. Centra were sagittally sectioned immediately adjacent to the center of the focus and then cut again approximately 1.5 mm off-center by using an Isomet rotary diamond saw (Buehler, Lake Bluff, IL). The sections were pressed between two pieces of Plexiglas (to prevent warping), air-dried for 24 h under a ventilation hood, and then mounted onto microscope slides with a mounting medium. After drying, sections were polished with wet fine grit (320-, 400-, and 600-grit) sand paper to approximately 0.5 mm and air-dried. Sections were viewed by using a binocular dissecting microscope with transmitted light.

Centrum radius (CR) and distance to the outer margin of each ring were measured to the nearest 0.001 mm along a straight line from the central focus to the center of the outer margin of the corpus calcareum (Fig. 1A) using a compound video microscope with the Optimus image analysis system (Media Cybernetics, vers. 6.5., Silver Spring, MD). PCL was plotted against CR to determine the proportional relationship between somatic and vertebral growth.

A banding pattern was readily distinguishable in sectioned centra; wide bands were separated by distinct narrow opaque bands. This pattern occurred on both arms of the corpus calcareum and extended across the intermedialia. Each pair of wide-narrow bands was considered a growth cycle; the narrow opaque bands, hereafter referred to as "rings," were counted (Fig. 1A). An angle change in the intermedialia and a ring on the corpus calcareum were present approximately 5 to 6 mm from the focus of each centrum and were considered to represent a birthmark. The "prebirth ring" reported by Nagasawa (1998) was present in most specimens just prior to the birthmark but was not counted nor measured (Fig. 1A).[3] A distinct notch was usually

[1] Goldman, K. J., and J. A. Musick. 2002. Unpubl. data. Alaska Department of Fish and Game, 3298 Douglas Pl., Homer, AK 99603, and Virginia Institute of Marine Science, 1208 Greate Rd. Gloucester Pt., VA 23062.

[2] Gaichas, S. 2002. Personal commun. NMFS Alaska Fisheries Science Center, 7600 Sand Point Way NE, Building 4, Seattle WA 98115.

[3] Our aging protocol was independently developed by the senior author and a co-reader, and later found to be identical to that used for salmon sharks in the western North Pacific (H. Nakano, pers. commun.) Vertebral images were exchanged and aged by the senior author and H. Nakano (and read randomly and blindly). The results validated that aging was conducted in an identical manner between studies.

present along the inside edge of the corpus calcareum at each ring, providing an additional aging feature, particularly in sections where the cut excluded the radials of the intermedialia (Fig. 1B). Annulus measurements were made from the origin of a wide band to the outer margin of the adjacent narrow band.

Two readers independently aged all centra two times in blind, randomized trials. This procedure allowed the calculation of within-reader precision, and between-reader precision twice. When there was a disagreement between readers, a final age determination was made by both readers viewing the centrum together. Percent agreement ($PA=[No.\ agreed/No.\ read]\times 100$), and percent agreement plus or minus one year ($PA\ [\pm 1\ yr]$) were calculated for length groups of 10 cm to test for precision. The criticism of percent agreement as a measure of precision has been that it varies widely among species and ages within a species (Beamish and Fournier, 1981; Campana, 2001). The criticism regarding variation among species is irrelevant because one is only interested in the particular species one is aging (i.e., these particular species are not compared among other species), but the criticism regarding variation of ages within a species is not only relevant, but is true. There is, however, validity in using percent agreement with individuals grouped by length as a test of precision because it does not rely on ages (which have been estimated), but rather on lengths, which are empirical values (Goldman, 2004; Cailliet and Goldman, 2004). Ages could be used if, and only if, all age classes have been validated.

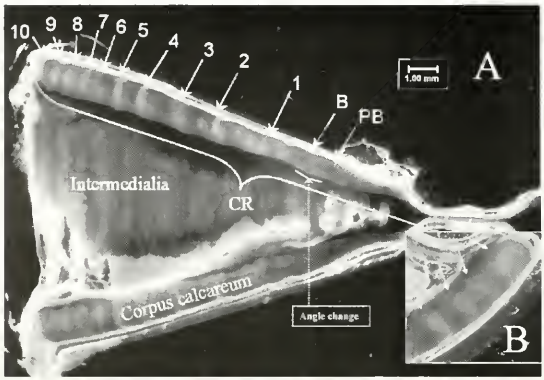

Figure 1

(**A**) Sagittal section of a 10-yr-old salmon shark (*Lamna ditropis*) vertebral centrum showing typical banding pattern. CR=centrum radius. (**B**) Portion of a sagittal section from a salmon shark vertebral centrum without intermedialia, showing the distinct notching pattern (white arrows) that accompanies the banding pattern and that is used to aid in assessing ages. The 1.0-mm bar applies to both A and B. PB = prebirth ring, B = birth ring and numbers indicate rings or age in years.

The most commonly used methods for evaluating precision among age determinations have been the average percent error (APE) technique of Beamish and Fournier (1981) and the modification of their method by Chang (1982). However, Hoenig et al. (1995) have demonstrated (using the Beamish and Fournier, 1981, data) that there can be differences in precision that these methods obscure because with the APE it is assumed that the variability among observations of individual fish can be averaged over all age groups and that this variability can be expressed in relative terms. Also, APE indices do not result in values that are independent of the age estimates, do not test for systematic differences, and do not distinguish all sources of variability (such as differences in precision with age) (Hoenig et al., 1995). Good APE values appear to tell us only which reader was less variable, not which was better or if either was biased, which is more critical in knowing whether reliable ages can be produced and replicated (i.e. is the error within and between readers due to random error or a systematic bias).

Campana et al. (1995) stated the importance of a separate measure for bias, and Hoenig et al. (1995) and Evans and Hoenig (1998) suggested testing for systematic differences between readers using chi-square tests of symmetry to determine whether differences are systematic (biased) or due to random error. These are statistically rigorous and effective methods for detecting bias (Campana, 2001) and were conducted in the present study. These techniques place all age values in contingency tables and test the hypothesis that values in a given table are symmetrical about the main diagonal (Hoenig et al., 1995; Evans and Hoenig, 1998). They can also be set up to test among all individual age classes or groups of age classes (Hoenig et al., 1995). The test statistic (the chi-square variable) will tend to be large if a systematic difference exists between the two readers.

A relative marginal increment (RMI) analysis was used to verify the temporal periodicity of ring formation in the vertebrae. This is a standardized marginal increment analysis whereby the margin, or growth area of a centrum from the last narrow growth ring to the centrum edge, is divided by the width of the last fully formed growth increment (Branstetter and Musick, 1994; Conrath et al., 2002). Resulting RMI values were compared to the month of capture. This analysis was performed on immature and mature sharks separately and combined. Age-zero animals were not included (because they have no fully formed increments).

The von Bertalanffy growth function was fitted to the vertebral age-at-length data for salmon sharks from the ENP with a nonlinear least squares regression algorithm ("nls" in S-Plus, Professional Release 1, Math-

soft Inc., Seattle, WA) to estimate parameters. The von Bertalanffy growth function is

$$L_t = L_\infty\left[1-\exp(-k(t-t_0))\right],$$

where L_t = length at age 't';
L_∞ = asymptotic or maximum length;
k = the growth coefficient; and
t_0 = age or time when length theoretically equals zero.

Growth parameters were estimated for the sexes separately and combined. A likelihood ratio test was used to determine whether differences between female and male growth parameters were significant or if a single set of growth parameters described the data better (Kimura, 1980; Quinn and Deriso, 1999; Haddon, 2001) (SAS, vers. 8.0, SAS, Cary, NC).

Back-calculation is a method for describing the growth history of each individual sampled, and numerous variations in methods exist (see Francis, 1990, for a thorough review and Goldman, 2004, for a description and application to elasmobranchs). Back-calculations estimate lengths-at-previous-ages for each individual and should be used if sample sizes are small and if samples have not been obtained from each month (Goldman, 2004; Cailliet and Goldman, 2004). Cailliet and Goldman (2004) stated "the proportional relationship between animal length or disk width and the radius of the vertebral centrum among different length animals within a population is used as a basis for empirical relationships regarding population and individual growth, as is the distance from the focus to each annulus within a given centrum." Hence, choosing the appropriate method (based on the relationship between animal length or disk width and the radius of the vertebral centrum) is critical if back-calculated data are to be used for obtaining accurate life history parameter estimates from growth function models. Because smaller size classes were not well represented in our female sample and because our male sample size was small, lengths at previous ages were back-calculated from centrum measurements for both sexes and fitted with the von Bertalanffy growth function.

The relationship between CR and PCL for ENP salmon sharks was used to determine the most appropriate method for back-calculating previous length-at-age. To our knowledge, however, no studies on elasmobranch fishes have examined multiple back-calculation methods for statistical or biological accuracy in relation to vertebral sample data. To that end, four different proportion methods were used and compared with our sample length-at-age data. We first applied the standard Dahl-Lea direct proportions method (Carlander, 1969):

$$L_i(L_c/CR_c)\times CR_i, \qquad (1)$$

where L_i = length at ring 'i';
L_c = length at capture;
CR_c = centrum radius at capture; and
CR_i = centrum radius at ring 'i'.

Next, we applied two modified versions of the Dahl-Lea method that use parameter estimates from the specific linear and quadratic fits that described the PCL-CR relationship. The linear-modified Dahl-Lea method (Francis, 1990) is

$$L_i = L_c\times\left[(a+bCR_i)/(a+bCR_c)\right], \qquad (2)$$

where 'a' and 'b' are the linear fitted parameter estimates. The quadratic-modified Dahl-Lea method (Francis, 1990) is

$$L_i = L_c\times\left[(a+bCR_i+cCR_i^2)/(a+bCR_c+cCR_c^2)\right], \qquad (3)$$

where 'a,' 'b,' and 'c' are the quadratic-fitted parameter estimates.

Ricker (1992) applauded Francis's (1990) back-calculation review paper, but like Campana (1990) suggested that the point of origin of proportional back-calculations should be related to a biologically derived intercept (i.e., length at birth). We, therefore, also applied Campana's (1990) "size-at-birth-modified" Fraser-Lee equation:

$$L_i = L_c+\left[(CR_i-CR_c)\times(L_c-L_{Birth})/(CR_c-CR_{Birth})\right], \qquad (4)$$

where L_{Birth} = length at birth; and
CR_{Birth} = centrum radius at birth. (Based on Tanaka, 1980, 62.5 cm PCL was used for L_{Birth}.)

Von Bertalanffy growth parameter estimates were obtained from all individual and mean back-calculated length-at-age, and from a combination of back-calculated lengths-at-age and our sample data. A likelihood ratio test was used for all scenarios to determine whether differences between female and male growth parameters were significant or if a single set of growth parameters described the data better (Kimura, 1980; Quinn and Deriso, 1999; Haddon, 2001) (SAS vers. 8.0, SAS, Cary, NC). Back-calculated length-at-age results from all four methods were examined to see which best reflected our vertebral sample data.

The reproductive tracts of 64 female and 14 male salmon sharks were examined visually to assess their reproductive status. Females ranged in size from 71 to 209 cm PCL, and males ranged from 63 to 187 cm PCL. Clasper lengths were obtained from 12 of the males (from 91 to 187 cm PCL). Gross analysis of reproductive tracts and maturity determinations were made according to the methods of Pratt (1988), Gilmore (1993), Pratt and Tanaka (1994), Hamlett (1999) and Hamlett and Koob (1999).

Median precaudal length-at-maturity (MPCL) was determined by first coding female (n=64) and male (n=14) maturity data into binary form, with 0=immature and 1=mature. The binary data were fitted with a logistic regression model ("GLM" in S-Plus, Professional Release 1, Mathsoft Inc., Seattle, WA). The median precaudal length-at-maturity was then estimated as

$MPCL = -a/b$ (a=intercept, b=slope) (Mollet et al., 2000; Neer and Cailliet, 2001; Conrath and Musick, 2002; Conrath, 2004). To estimate percent maturity by length for the ENP salmon shark population, the 'a' and 'b' estimates (from the "GLM" model) were substituted into the equation; *percent mature* = $100 \times [(e^{(a+b \times length)})/(1+e^{(a+b \times length)})]$, and plotted against *PCL*. A nonparametric bootstrap (n=1000 replications) was conducted with S-Plus and 95% confidence limits were obtained from the 2.5th and 97.5th empirical percentiles.

Sperm storage in the oviducal gland has been documented in several shark species (Pratt, 1993). Oviducal glands were taken from six mature females, ranging in size from 180 to 192 cm PCL, caught in PWS waters in late July and late August, to determine the presence or absence of sperm. Samples were initially fixed in 10% formalin. Samples were rinsed extensively to remove fixative and then stored in 70% ethanol. Cross-sections along the entire length of each gland were trimmed, dehydrated in a graded series of ethanol, cleared in a limonene-based solvent, infiltrated with paraffin, and embedded in paraffin blocks. Serial sections (5 um) were prepared by using a rotary microtome, mounted onto poly-L-lysine-coated slides, dried, deparaffinized, rehydrated, and stained by using standard Harris hemotoxylin and eosin in order to examine general cellular detail (Hinton, 1990). Sections were examined for the presence of sperm by using a compound microscope at magnifications ranging from 100× to 1000×.

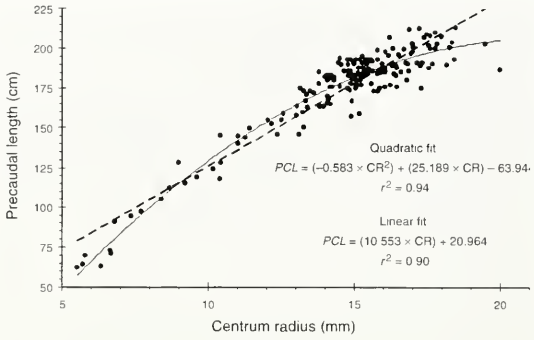

Figure 2

Relationship between centrum radius and precaudal length for eastern North Pacific salmon sharks (*Lamna ditropis*) showing significant fits given by linear and quadratic equations (sexes combined, n=182). PCL = precaudal length, CR = centrum radius.

Results

Length and weight equations

One hundred sixty-six of the 182 salmon sharks in this study were female, resulting in a F:M sex ratio of 10.4/1. Although females dominated our sample, the following equations for converting PCL into FL and TL appear to work equally well for both sexes.

$FL = 1.08 \times PCL + 6.91$ (r^2=0.99; n=138)

$TL = 1.15 \times PCL + 15.19$ (r^2=0.97; n=133).

Weight-length relationships for female and male salmon sharks we sampled in the ENP were $W = 8.2 \times 10^{-05} \times L^{2.759}$ (r^2=0.99, n=20) and $W = 3.2 \times 10^{-06} \times L^{3.383}$ (r^2=0.99, n=7) respectively, and $4.4 \times 10^{-05} \times L^{2.875}$ (r^2=0.99) for the sexes combined. A likelihood ratio test showed that separate equations for each sex describe the data better than a single equation for the sexes combined (χ^2=12.1; df=3; P<0.01).

Vertebral analysis

There was a slight curvilinear relationship between centrum radius (CR) and shark PCL (Fig. 2). A linear regression gave a significant fit to the data ($PCL = (10.553 \times CR) + 20.964$; r^2=0.90; P<0.0001); however, a quadratic equation produced a slightly better fit ($PCL = -63.944 + (25.189 \times CR) - (0.583 \times CR^2)$; r^2=0.94; P<0.0001) and a t-test showed the third parameter to be statistically significantly different from zero (t=10.32; df=181, P<0.0001). However, it was necessary to compare the mean back-calculated results from Equations 1 through 4 with the mean sample PCL data to see if the slightly better statistical fit of the quadratic equation translated into better biological accuracy for modeling growth.

Percent agreement (PA) among readers was 68.1% for the first set of blind reads and 72.0% for the second set, and the within-reader PA was 79.7% for reader one (the lead author) and 75.3% for reader two. Percent agreement (±one yr) was >95% for all reader comparisons. Agreement between and within reader age assessments was 100% until age 7 or 8, depending on the reader comparison. When grouped by 10-cm length increments, percent agreement was 100% for sharks ≤160 cm PCL, and 100% ±1 yr for sharks ≤180 cm PCL (Table 1). (PA and PA ±1 for length groups were virtually the same for both sets of between-reader comparisons, but slight differences occurred above 160 and 180 cm PCL, respectively.) The chi-square tests of symmetry gave no indication that differences between and within readers were systematic rather than due to random error (χ^2 test, P>0.05 in all cases).

Relative marginal increment (RMI) analysis showed that postnatal rings form annually between January and March. The smallest relative margins occurred in

Table 1

Percent agreement (PA) and PA ± one year, from the second set of "reads," for eastern North Pacific salmon sharks (*Lamna ditropis*) when placed into 10-cm precaudal length (PCL) groups.

PCL (cm)	Total no. read	No. agreed upon	No. agreed upon ±1	PA	PA ±1
60–70	5	5	5	100	100
70.1–80	2	2	2	100	100
80.1–90	0	—	—	—	—
90.1–100	4	4	4	100	100
100.1–110	1	1	1	100	100
110.1–120	5	5	5	100	100
120.1–130	3	3	3	100	100
130.1–140	1	1	1	100	100
140.1–150	6	6	6	100	100
150.1–160	9	9	9	100	100
160.1–170	11	8	11	72.7	100
170.1–180	30	22	30	73.3	100
180.1–190	55	38	53	69.1	96.4
190.1–200	34	22	32	64.7	94.1
200.1–210	12	4	10	33.3	83.3
>210	4	1	3	25.0	75.0
n	182	131	175	—	—
Percent agreement	—	—	—	72.0	96.2

February and March, followed by a consistent increase in RMI, and the largest relative margins occurred in December and January. There was no difference in this trend when immature and mature sharks were examined separately; therefore all ages classes were combined (Fig. 3).

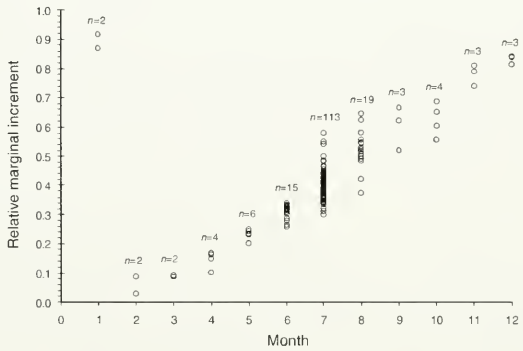

Figure 3

Results of relative marginal increment analysis showing that annulus formation occurs between January and March (n=176).

Vertebral age-at-length data from 166 female salmon sharks provided von Bertalanffy parameters of L_∞=207.4 cm *PCL*, k=0.17/yr, and t_0=−2.3 years (Fig. 4). When the von Bertalanffy growth function was fitted to the quadratic-modified Dahl-Lea back-calculations for females, the life history parameters were similar to those produced from the sample length data (Table 2). Vertebral age data from 16 males provided von Bertalanffy parameters of L_∞=182.8 cm PCL, k=0.23/yr, and t_0=−1.9 years (Fig. 4). Back-calculated lengths-at-age for male salmon sharks, either with or without sample data included, provided slightly lower k coefficients (=0.20), but similar L_∞ and t_0 parameters (Table 2). Vertebral age data for the sexes combined (n=182) provided von Bertalanffy parameters of L_∞=204.5 cm PCL, k=0.18/yr , and t_0=−2.2 years. A likelihood ratio test showed that separate von Bertalanffy growth models describe the data better for each sex than one model with the sexes combined (χ^2=29.1; df=3; P<0.001).

The quadratic-modified Dahl-Lea method (Eq. 3) represented most accurately the mean sample precaudal length-at-age data. It produced mean back-calculated lengths-at-age within 4.2 cm of mean sample lengths-at-age for female salmon sharks >120 cm PCL and within 8.8 cm for females <120 cm PCL (Fig. 5A). When applied to males, Equation 3 produced mean back-calculated lengths-at-age within 10 cm of mean sample lengths-at-age for sharks <120 cm PCL and >150 cm

Table 2

Von Bertalanffy growth parameters for female, male, and sexes combined for salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific. Numbers in parentheses are standard errors. * = not independent.

	L_∞	k	t_0
Eastern North Pacific (present study)			
Females			
Vertebral sample data (n=166)	207.4 (2.5)	0.17 (0.01)	−2.3 (0.2)
Back-calculations (n=1814*)	205.3 (0.9)	0.18 (0.002)	−2.0 (0.03)
Mean back-calculation (n=21*)	210.0 (1.1)	0.17 (0.004)	−2.1 (0.09)
Back-calculations with sample data (n=1980*)	206.0 (0.8)	0.18 (0.002)	−2.0 (0.03)
Males			
Vertebral sample data (n=16)	182.8 (3.7)	0.23 (0.03)	−1.9 (0.3)
Back-calculations (n=161*)	183.9 (2.0)	0.20 (0.008)	−2.0 (0.1)
Back-calculations with sample data (n=177*)	184.2 (1.9)	0.20 (0.008)	−2.0 (0.1)
Combined			
Vertebral sample data (n=182)	204.5 (2.4)	0.18 (0.01)	−2.2 (0.2)
Western North Pacific (Tanaka, 1980)			
Females			
Vertebral sample data	203.8	0.14	−3.9
Males			
Vertebral sample data	180.0	0.17	−3.6

PCL. In between those lengths, however, the deviation from mean sample length-at-age increased to 16.5 cm (Fig. 5B). (The larger deviations for males were likely the result of the small sample size.) Lee's phenomenon did not occur in either sex with the quadratic-modified Dahl-Lea method.

Of the 64 female salmon shark reproductive tracts examined, 55 were fully mature, and 11 of the 14 males examined were mature. Mature female reproductive tracts consisted of a well-developed right ovary (the only functional ovary in lamniform sharks) containing various sizes of ova, large oviducts and oviducal glands, and expanded, heavily striated uteri with thickened walls. In stark contrast, the right ovary from immature female reproductive tracts was considerably smaller and had no signs of developing ova, the oviducal gland was virtually indistinguishable from the oviduct, and the uteri were extremely small, thin-walled, flaccid and completely smooth. Additionally, the epigonal organ in mature females was large and extended 2/3 the length of the uteri, whereas in immature females it was small and generally did not extend much past the anterior end of the uteri. No females examined were of an "intermediate"reproductive nature. Mature male reproductive tracts consisted of large well-developed testes, a thick epididymis leading to a coiled ductus deferens, rigid (fully calcified) claspers and well-developed siphon sacs. Immature male reproductive tracts consisted of small testes that were partially embedded in the epigonal organ, thin epididymis and straight ductus deferens, nonrigid claspers and poorly developed siphon sacs.

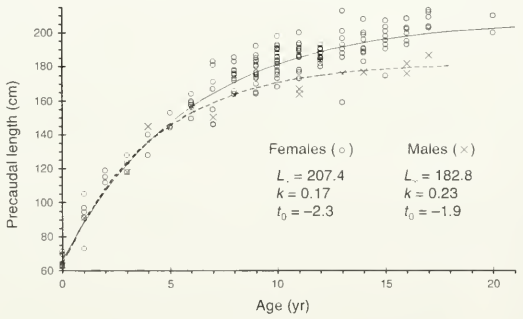

Figure 4

Von Bertalanffy growth curves fitted to female (n=166) and male (n=16) vertebral sample data for eastern North Pacific salmon sharks (*Lamna ditropis*). Estimates for parameters of the von Bertalanffy growth function are summarized.

Estimated median precaudal length-at-maturity (MPCL) for ENP female and male salmon sharks were 164.7 cm PCL and 124.0 cm PCL, respectively (Fig. 6). The smallest mature female observed was 164.0 cm PCL, and the largest immature female observed was 176.5 cm PCL (however, all other immature females were ≤163 cm PCL). None of

Table 3

Mean ages and precaudal lengths (PCL) for eastern North Pacific salmon sharks (*Lamna ditropis*) by location. CA = California; seAK = southeast Alaska.

	Females			Males		
	CA to seAK	Alaska	Combined	CA to seAK	Alaska	Combined
Age (yr)						
Mean	2	11	10	3	12	9
Range	0–5	5–20	0–20	0–7	6–17	0–17
PCL (cm)						
Mean	103.6	184.7	175.0	113.5	171.9	153.7
Range	62.2–153	144.8–213.4	62.2–213.4	63–150.5	155.4–187	63–187
n	20	146	166	5	11	16

the oviducal glands sampled from mature females contained spermatozoa. The smallest mature male observed was 155.4 cm PCL, and the largest immature male was 91.0 cm PCL. Based on age estimates from vertebral sample data, ages at MPCL range from 6 to 9 yr for females and from 3 to 5 yr for males. Ninety-five percent confidence limits (for percent mature) were very narrow for females <155 cm PCL and >172.5 cm PCL and for males <107.5 cm PCL and >132.5 cm PCL. The wide vertical confidence intervals around the calculated estimates of MPCL (Fig. 6) were caused by not having many observations for lengths around the estimated MPCL in the sample.

Age-length composition in the Eastern North Pacific

The mean age and length composition of ENP salmon sharks was latitude dependent (Table 3). Sharks between 0 and 7 yrs old, ranging from 62.2 to 153 cm PCL, were collected from southern California to southeast Alaska, with smaller individuals found in the southern part of that range. Sharks between 5 and 20 yrs old, ranging from 144.8 to 213.4 cm PCL, were collected from southeast Alaska up into the Gulf of Alaska, Prince William Sound, and the Bering Sea.

Discussion

Vertebral growth significantly increased with somatic growth (Fig. 2), which, along with the reliability of the RMI analysis

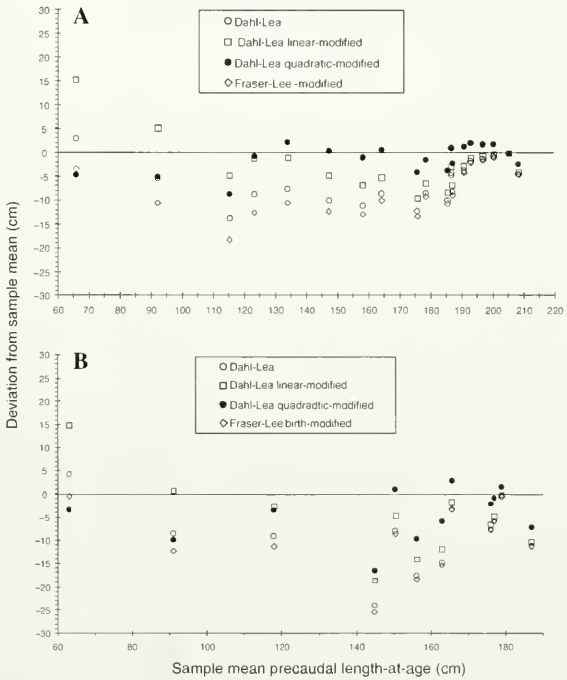

Figure 5

Mean deviation, from mean sampled precaudal length, of four proportional back-calculation methods for (**A**) female, and for (**B**) male eastern North Pacific salmon sharks (*Lamna ditropis*). Data points represent mean back-calculated lengths-at-age. An *x*-axis point on the zero line extending from the y-axis would represent zero deviation from the sample mean length-at-age.

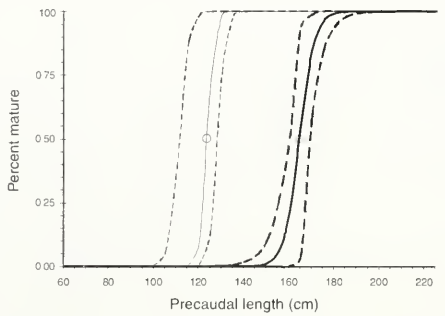

Figure 6

Percent versus precaudal length curves for eastern North Pacific female (heavy lines) and male (light lines) salmon sharks (*Lamna ditropis*) with 95% confidence bands on percent mature. Diamond and circle show estimates of median precaudal length at maturity (MPCL) for females and males respectively. Confidence bands (dotted lines) are 2.5th and 97.5th empirical percentiles obtained by bootstrapping.

(Fig. 3), demonstrates that vertebral growth patterns are a reliable indicator of age in salmon sharks. Precision was high between and within readers with limited differences (Table 1) that were attributable to random error. These results provided us with a high degree of confidence in the age assessments determined from the von Bertalanffy growth model (with vertebral sample data), and hence in the resulting life history parameter estimates.

Tanaka (1980) and Nagasawa (1998) stated that salmon sharks produce one ring per year, but a RMI analysis was not provided in their studies. Our RMI analysis verified an annual periodicity of banding patterns for salmon sharks, ranging from 73 cm to 213.4 cm PCL and encompassing ages 1 to 20 for females and ages 1 to 17 for males. The major period of growth occurs from May through November, slowing some as January approaches (Fig. 3). A brief cessation, or extreme slowing, of growth (ring formation) occurs between January and March, and growth increases again in April–May. Although we were able to examine specimens from every month of the year, additional samples from December through April would enhance RMI precision.

The similar von Bertalanffy growth parameter estimates generated from female vertebral sample data, back-calculated data, and the combination of the two indicated that sample size was sufficiently large and encompassed the known size range of the species. Von Bertalanffy parameters for males would have been improved with a larger sample size that would have reduced the difference between values of 'k' from vertebral sample and back-calculated data (Table 2). More samples would likely have had little influence on L_∞ for either sex because salmon sharks close to maximum length were examined in the present study. It is possible that the discrepancy between female and male sample sizes could have influenced the outcome of the likelihood ratio test. However, with the differences in observed maximum length (and estimated L_∞) between the sexes and the small standard errors associated with the male von Bertalanffy estimates (Table 2), it is unlikely that an increased male sample size would have altered the test result.

The error associated with back-calculated length *versus* the actual length at a given age has been a focal point of papers by Campana (1990), Francis (1990) and Ricker (1992) and prompted our evaluation of several proportional back-calculation methods. There was a statistically valid reason for using the quadratic-modified Dahl-Lea (Eq. 3) over the linear-modified Dahl-Lea (Eq. 2) (see "Results" section); however, the only way to cross-compare all four back-calculation methods in a biologically meaningful way was to apply all of them to the vertebral sample data. Both modified Dahl-Lea equations were more accurate in representing the mean sample length-at-age data than the standard Dahl-Lea or the size-at-birth-modified Fraser-Lee equations (Fig. 5, A and B). However, the quadratic-modified Dahl-Lea was the best predictor of prior length-at-age (i.e., best resembled our vertebral sample length-at-age data). Although these back-calculation results are, of course, dependent on the assumption that growth has not significantly changed over time, and are applicable only to salmon sharks, they demonstrate the importance of choosing the appropriate method to minimize error, which results in a greater ability to accurately model growth. Accurate growth parameters will result in more accurate demographic parameters and stock assessments, leading to more responsible management. Even greater confidence could be achieved if animals collected in the past were available because they would allow a direct comparison of size-at-age then and now in order to verify that the growth rate for the salmon shark has not changed.

Our results show that salmon sharks in the ENP attain their maximum size at a faster rate (k) than those from the WNP (Table 2). We were unable to test the statistical significance of these differences because neither Tanaka (1980) nor Nagasawa (1998) provided point estimates and standard error values for their WNP data. There were, however, significant resultant biological differences present. Both female and male salmon sharks reach first age at sexual maturity approximately 2 years earlier in the ENP than in the WNP. Female salmon sharks in the WNP mature between 8 and 10 years of age (Tanaka, 1980; Nagasawa, 1998). From the reproductive tracts examined, we found that female salmon sharks in the ENP reach sexual maturity between ages 6 and 9. Although age at first maturity was earlier in the ENP, length at maturity appears to be similar; 160–180 cm PCL in the WNP, and a MPCL = 164.7 cm PCL in the ENP (Fig. 6). Male salmon sharks in the WNP mature at approximately

5 years of age and 140 cm PCL (Tanaka, 1980; Nagasawa, 1998). From our small sample size, the logistic method provided an estimate that male salmon sharks in the ENP mature between the ages of 3 and 5, and MPCL=124.0 cm PCL (Fig. 6). Clasper lengths did not enhance the ability to determine male length at sexual maturity because specimens around the calculated MPCL were not sampled. Although the MPCL for males indicates a smaller length at maturity, our confidence in the accuracy of the male MPCL estimate (due to sample size) is low (Fig. 6).

The lack of spermatozoa in any of the oviducal gland samples analyzed is not surprising considering no lamniform shark examined to date has shown evidence of sperm storage (Pratt, 1993). However, specimens we examined were specifically chosen from the time period of late July through late August when mating was likely to have been taking place (Goldman and Human, 2005; Goldman and Musick, in press). A larger sample size taken through that time period and extending through September may resolve the question better regarding the suspected residence time of sperm in the oviducal gland of lamniform sharks—a residence time that is probably only a few days timed with actual mating activity (Pratt, 1993). The large number of eggs produced to feed oophagous young (Wourms, 1977; Gilmore et al., 1983; Gilmore, 1993) could have "flushed" any stored sperm out of the oviducal gland (Pratt, 1993).

In the WNP, salmon sharks are born in the spring of the year and pups range in length from 60 to 70 cm PCL (Tanaka, 1980; JAMARC, 1980; Nagasawa, 1998). Litter size in the WNP is up to 5 pups, and the ratio of male to female is 2.2:1 (Tanaka, 1980). Our data support a similar timing for pupping and for length at birth in the ENP, but no pregnant females were taken during the course of our research and therefore information on litter size and pup sex ratio is not available for the ENP.

Nagasawa (1998) characterized salmon shark growth through age ten as follows; after birth, "they grow to between 90 and 105 cm PCL by the next spring ... subsequent annual growth is 10–15 cm per year up to age-4 fish." He stated, in addition, that females and males attain an average length of 173 cm PCL and 163 cm PCL, respectively, by age 10. Our data indicated that the average growth rate (cm per year) for salmon sharks in the ENP is very similar to the rate in the WNP through age 4. By age 5, ENP females are growing at a considerably faster rate than WNP females, reaching an average of 185.4 cm PCL by age 10 (Table 4). Male salmon sharks in the ENP appear to begin outgrowing their WNP counterparts by age 4 (Table 4). Salmon shark longevity appears to be similar in the ENP and WNP. Maximum observed age for females in our study was 20, whereas it was 17 in the WNP (Tanaka, 1980); however, maximum observed age for males was only 17, whereas it was 25 for the WNP. We were unable to obtain samples of male salmon sharks at or near maximum age because of our small sample size.

Salmon sharks in the ENP and WNP attain the same maximum length (about 215 cm PCL for females and about 190 cm PCL for males). However, WNP salmon sharks take longer to reach a given length than those in the ENP (Table 4). Additionally, the weights for the same length females and males are considerably different except at male maximum length, which appears to be equivalent to females of similar length. Our data indicate that the weight-at-length differences between ENP and WNP salmon sharks begin at approximately 110 cm PCL for females, and at 140 cm PCL for males (Fig. 7, A and B). Although a greater sample size could enhanced precision and may alter the equations presented in the present study to some degree, the data show that weight-at-length is particularly greater for adult salmon sharks in the ENP than in the WNP. As with the von Bertalanffy growth models, it is possible that the discrepancy between female and male sample sizes may have influenced the outcome of the likelihood ratio test. However, the sample-size discrepancy was not as large as with the growth curve data and standard errors were small for both sexes; therefore it is unlikely that an increased male sample size would have altered the test result.

Although season and size at birth appear to be similar for salmon sharks in the ENP and WNP, the locations where females pup are different. A salmon shark pupping and nursery ground exists along the transitional boundary of the subarctic and central Pacific currents (Nakano and Nagasawa, 1996). Our data indicate that a second pupping and nursery ground exists, ranging from southeast Alaska to the northern end of Baja California, Mexico (central California being the most common area for ages zero and one [see Table 3]). Ages zero through 5 were caught only between southern California and southeast Alaska, and ages 5 and above were caught only in Alaska waters. The latitudinal size segregation observed in the ENP indicates that pregnant females may move south along the California coast to give birth in the spring.

The high degree of sexual segregation across the Pacific Basin (Nagasawa, 1998; Goldman and Musick, in press), along with the age- and length-dependent latitudinal distribution are important factors in pursuing responsible management and conservation of the salmon shark. Although latitudinal migrations and movements are documented in this species (Iino, 1939; Kosugi and Tsuchisaki, 1950; Tanaka, 1980; Balgaderov, 1994; Nakano and Nagasawa, 1994; Weng et al., 2005), they are still poorly understood. Similarly, although trans-Pacific movements have been inferred from fisheries bycatch data (Goldman and Musick, in press), there has yet to be documentation of individuals moving across the North Pacific. However, the degree of the sexual segregation by itself (in regard to finding a mate) would seem to indicate that movements across the Pacific are likely.

Another critical element for successful management of salmon sharks is stock structure, which is not well understood at this time; however a study of population

Table 4

Mean precaudal length (PCL) at age for salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific (ENP and WNP). Ranges (or individual lengths for some males) are given for sharks from the present study.

	Females			Males	
Age	WNP* mean PCL	ENP mean PCL	ENP range	WNP* mean	ENP individual or range
0	62.5	65.9	62.2–71.1	62.5	63.0
1	97.5	92.1	73.0–105.0	97.5	91.0
2	110.0	115.3	112.0–119.0	110.0	—
3	122.5	123.3	118.0–128.0	122.5	118.0
4	135.0	134.0	128.0–140.0	135.0	145.0
5	141.3	147.3	144.0–153.0	139.7	—
6	147.7	158.1	149.7–164.0	144.3	155.4–157.0
7	154.0	164.1	145.9–183.0	149.0	150.5
8	160.3	175.7	164.0–185.4	153.7	163.0
9	166.7	178.4	164.0–192.0	158.3	—
10	173.0	185.4	168.0–198.0	163.0	—
11	177.4	187.0	173.0–200.0	164.2	164.0–176.0
12	181.8	186.7	180.0–193.0	165.3	187.0
13	186.2	190.8	159.9–213.0	166.5	176.0
14	190.6	192.9	183.0–208.0	167.6	177.0
15	195.0	196.7	175.0–207.1	168.8	—
16	199.4	200.1	193.0–208.3	169.9	176.0–182.0
17	203.8	208.3	203.0–213.4	171.1	187.0
18	—	—	—	172.2	—
19	—	—	—	173.4	—
20	—	205.1	200.0–210.2	174.5	—
21	—	—	—	175.7	—
22	—	—	—	176.8	—
23	—	—	—	178.0	—
24	—	—	—	179.1	—
25	—	—	—	180.3	—

* Mean length-at-age for WNP calculated from information in Nagasawa (1998). L_∞ was used as mean length at age 17 for females and as mean length at 25 for males.

genetics is currently underway. Current information from the western and central North Pacific implies that salmon sharks constitute a single stock, but there is no current information for the Japan Sea or the eastern North Pacific (Sano, 1962; Tanaka, 1980; Blagoderov, 1994; Nagasawa, 1998). New technologies such as archival and pop-up satellite transmitters should provide documentation of movements and migrations (Weng et al., 2005) and key information as to whether regional or international conservation and management plans are needed.

Stock structure may be an important factor in the differential growth rates between ENP and WNP salmon sharks. However, ecological differences between the ENP and WNP could also be responsible for the observed differences. Young salmon sharks appear to move from temperate waters of the U.S. west coast into the Alaska Gyre and the Gulf of Alaska as they approach adulthood, which is when their growth rate begins to exceed that of their WNP counterparts. These waters are extremely productive (Strub et al. 2001), and abundant food resources may be the key factor in the differences in growth rate, age-at-maturity, and weight-at-length observed between ENP and WNP salmon sharks.

A high degree of variability exists in the periodicity of ring and growth band formation within and among taxonomic groups of elasmobranchs, and much of the variation observed in several lamniform sharks has not yet been explained (Branstetter, 1990; Branstetter and Musick, 1994; Wintner and Cliff, 1999). For example, Cailliet et al. (1983) stated that shortfin mako sharks (*Isurus oxyrinchus*) from the Pacific appear to form growth rings annually, whereas Pratt and Casey (1983) stated that Atlantic specimens appeared to produce two

rings per year. However, validation of single annual ring (band pair) deposition has now been demonstrated from recaptures of oxytetracycline(OTC)-injected mako sharks (Natanson et al., in press), as well as with a new technique where bomb radiocarbon is used to validate ages in long-lived sharks (Campana et al., 2002; Ardizzone et al., in press).

Lamnid sharks are endothermic (Carey et al., 1985; Lowe and Goldman, 2001), and prior to the Campana et al. (2002) and Ardizzone (in press) radiocarbon studies, it appeared that lamnid sharks might possess fairly high growth rates (growth coefficient, k) compared to other sharks, particularly those that grow to a large size (Musick, 1999). However, with mako sharks now appearing to have a growth coefficient around 0.072/yr (sexes combined)(Cailliet et al. 1983), the validation of porbeagle shark (*Lamna nasus*) age and growth (k=0.06 and 0.08/yr for females and males, respectively) (Natanson et al. 2002), and estimates of white shark (*Carcharodon carcharias*) growth coefficients ranging from 0.058 to 0.071/yr (for sexes combined)(Cailliet et al., 1985; Wintner and Cliff, 1999; Malcolm et al. 2001), salmon sharks appear to be the species that possess the higher growth rates (Tanaka, 1980; present study). Salmon sharks are not only endothermic, but also appear to be homeothermic (i.e., defend a specific body core temperature regardless of ambient temperature) (Goldman et al., 2004). This uncommon physiological trait for a shark, combined with a diet that includes many lipid-rich species (e.g., salmonids), may influence the growth rate of this species, but endothermy does not appear to be correlated with faster growth rates in lamnid sharks (Goldman, 2002).

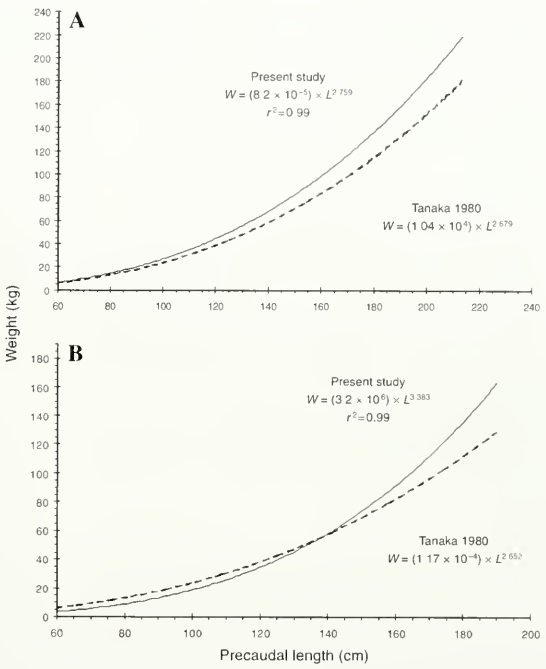

Figure 7

Comparison of weight-length relationships of eastern and western North Pacific salmon sharks (*Lamna ditropis*) (**A**) females, and (**B**) males. Western North Pacific data were obtained from Tanaka (1980) and Nagasawa (1998).

The most recent demographic analysis has indicated that salmon shark populations in the eastern and western North Pacific are stable at this time (Goldman, 2002) and current research is beginning to assess standing stock and population numbers, as well as examine the stock structure of salmon sharks in the eastern and western North Pacific in order to further responsible management of the species. The differences in growth rates and strong sexual segregation across the North Pacific basin and an unknown rate of current bycatch complicate management of this species.

Acknowledgments

We are grateful to the many people have helped in field and lab operations. We thank J. Castro, J. Herschleb and K. Herschleb of the FV *Pagan*, K. Anderson, B. Block, and L. Hulbert for assistance in the field. We thank R. Candopoulos, the crew, and many passengers aboard the FV *Legend* and B. Steffen (FV *Sea Sound*) for vertebral samples collected on sport fishing trips, and to the following Alaska Department of Fish and Game biologists for their logistic support, field help and overall assistance with our Alaska shark research: B. Bechtol, S. Meyer, C. Stock, M. Miller, D. Vincent-Lang, and D. Branshaw and D. Anderson of the RV *Montague*. We thank S. Anderson for his assistance with sample collection and unwavering endurance in the field, and J. Gelsleichter for the histological workup of the oviducal glands. We also thank J. DiCosimo (North Pacific Fishery Management Council) for her logistical support and assistance in the field. This research was supported in part by the National Geographic Society's Committee for Research and Exploration (grant no. 6714-00), Sigma-Xi, and the Lerner-Gray Fund for Marine Research. This research represents a portion of K.J. Goldman's Ph.D. dissertation conducted at the College of William and

Mary, School of Marine Science, Virginia Institute of Marine Science. This article is dedicated to the life and memory of Philip Goldman, compassionate human being and dedicated father.

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Potential causes of mortality for horseshoe crabs (*Limulus polyphemus*) during the biomedical bleeding process

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Biomedical companies catch and bleed horseshoe crabs for the production of *Limulus* amebocyte lysate (LAL), a product used for protecting public health (Berkson and Shuster, 1999). LAL is a clotting agent, derived solely from horseshoe crab blood cells, which is used to detect the presence of pathogenic gram-negative bacteria in injectable drugs and implantable medical and dental devices (Mikkelsen, 1988; Novitsky, 1991). In addition, LAL is used in many diagnostic tests for such illnesses as gram-negative bacterial meningitis and typhoid fever (Ding and Ho, 2001). Because the LAL test allows one to detect femtogram levels of endotoxin (Ding and Ho, 2001), it is the most effective test for detecting endotoxin contamination, and its increasing use in medical and pharmaceutical laboratories makes it a highly valued product.

The biomedical industry harvested approximately 260,000 horseshoe crabs in 1997 (HCTC[1]) for the production of LAL. By 2000, the number of horseshoe crabs bled had increased less than 1% (ASMFC[2]). However, approximately 25% of the horseshoe crabs landed for biomedical purposes were rejected for use, and about 45% of those rejected were rejected because they were injured (ASMFC[2]). Some mortality is likely related to harvest injuries, but this rate of mortality is unknown. At current harvest levels, mortalities from biomedical collection and bleeding methods may not be negligible. Mortalities inflicted by the biomedical industry on the horseshoe crab population come in addition to mortalities caused by the commercial fishery, where horseshoe crabs are harvested for use as bait for eel (*Anguilla rostrata*) and whelk (*Busycon* spp.) fisheries (Walls et al., 2002). Furthermore, numerous migratory shorebird species feed on horseshoe crab eggs (Clark, 1996) and adults (Botton and Loveland, 1989, 1993) to fuel their migration from South American wintering grounds to their Arctic breeding grounds (Clark, 1996). Concern has arisen over horseshoe crabs, in part because of local population declines, increased catch and effort, and the need for a superabundance of horseshoe crab eggs for shorebirds, all of which necessitate a conservative, risk-averse management approach (ASMFC[2]). It is important to not only investigate the effects of the commercial fishery harvest and natural predation on horseshoe crab stocks but to comprehensively assess the impact of the biomedical industry take on horseshoe crab population viability. Reducing mortalities from the biomedical industry may aid in conserving the horseshoe crab population, as well as in reducing the magnitude of conflict between this industry, the commercial fishery, and environmentalists. To achieve this goal, further investigation into the biomedical bleeding process and its effects is required.

Throughout the typical biomedical bleeding process, horseshoe crabs are subjected to a variety of potential stressors (i.e., air exposure, increased temperature, handling, blood loss, trauma, etc.). Each LAL producer has its own bleeding process involving different methods of capture, distance and method of travel to the bleeding facility, different holding times and conditions, different bleeding methods, and methods of returning bled crabs that are most appropriate to that company's location and facility set-up (Walls and Berkson, 2003). An example of one version of the biomedical bleeding process begins with the collection of the horseshoe crabs by trawling, dredge, or hand-harvest methods (HCTC[1]). Animals may be held on the deck of a boat or in containers for several hours during collection, transported to the bleeding facility in trucks (that may or may not be air-conditioned), held in the

[1] HCTC (Horseshoe Crab Technical Committee). 1998. Status of the horseshoe crab (*Limulus polyphemus*) population off the Atlantic Coast, 9 p + figures and tables. Horseshoe Crab Technical Committee, Atlantic States Marine Fisheries Commission, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[2] ASMFC (Atlantic States Marine Fisheries Commission). 2002. Review of the fishery management plan for horseshoe crab (*Limulus polyphemus*). Horseshoe Crab Plan Review Team, Atlantic States Marine Fisheries Commission, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

Manuscript submitted 17 May 2004
to the Scientific Editor's Office.

Manuscript approved for publication
21 July 2005 by the Scientific Editor.

Fish. Bull. 104:293–298 (2004).

cold room of a laboratory for several hours at an air temperature of 16–18°C, bled for a period of time, and then held in the coldroom or in a truck until transport back to the dock (Grogan[3]; Walls[4]). Horseshoe crabs that are returned to the ocean are transferred onto a boat and returned to their approximate point of capture within 72 hours of their collection (HCTC[1]). The numerous stressors to which the horseshoe crabs are exposed throughout the biomedical bleeding process likely have an effect on their mortality rates, both for horseshoe crabs used for bleeding and for those crabs collected, but rejected for use.

Additional sources of stress also may arise from the bleeding methods used by some biomedical companies. The bleeding protocols at some facilities involve gravitationally withdrawing blood from the heart (punctured with a large gauge needle) until blood flow slows to an intermittent drip (Grogan[3]; Walls[4]). One study reported a range of extracted blood to be from 8.4 mL to 218.7 mL in male horseshoe crabs (Walls, 2001) and up to 267.8 mL in females (Walls[5]). Unfortunately, biomedical companies do not know how much blood horseshoe crabs of a given size possess and how much can be safely extracted. Thus, extracting the reported upper ranges of blood volume from males and females may cause stress or mortality.

Several studies have estimated mortality associated with the biomedical bleeding process to be between 8% and 20% (Rudloe, 1983; Thompson, 1998; Kurz and James-Pirri, 2002; Walls and Berkson, 2003). These studies either simulated the biomedical bleeding process (Rudloe, 1983; Kurz and James-Pirri, 2002) or monitored mortality of a given number of horseshoe crabs bled by a biomedical company (Thompson, 1998; Walls and Berkson, 2003). Although the results provide information on mortality rates associated with a biomedical companies' procedures, they provide no guidance on how biomedical companies may reduce mortality rates.

Rather than quantifying mortality rates associated with the biomedical bleeding process as a whole, we isolated and tested certain elements of the bleeding process to gain information on the potential causes of mortality for horseshoe crabs used in the biomedical industry. The objectives of this study were 1) to quantify mortality associated with blood extraction at set levels and 2) to quantify mortality associated with stress from simulated transport and holding procedures, combined with the stress of blood extraction at the same levels as in the first objective.

[3] Grogan, W. 2003. Personal commun. Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State Univ., Blacksburg, VA 24061.

[4] Walls, B. 2001. Personal commun. Center for Environmental Studies, Virginia Commonwealth Univ., 1000 West Cary Street, Box 843050, Richmond, VA 23284.

[5] Walls, B. 2001. Unpubl. data. Center for Environmental Studies, Virginia Commonwealth Univ., 1000 West Cary Street, Box 843050, Richmond, VA 23284.

Methods

Adult horseshoe crabs were obtained from Cambrex BioScience Walkersville, Inc., a commercial biomedical company on 9 July and 28 August 2003. Horseshoe crabs were captured by using a standard trawling procedure off the coast of Ocean City, Maryland (Hata and Berkson, 2003). After capture, horseshoe crabs were transported in an air-conditioned van to the Horseshoe Crab Research Center (HCRC) at Virginia Polytechnic Institute and State University in Blacksburg, Virginia. The animals were maintained in a recirculating aquaculture system in appropriate environmental conditions (Brown and Clapper, 1981) and monitored daily, but not fed. The animals were acclimated to the aquaculture conditions for one week, during which time they were tagged, sexed, and measured. Tagging involved drilling two 3/32″ holes into the prosoma at its thinnest point and attaching a laminated oval fish tag (Floy Tag, Seattle, WA) with two 3/32″ wide cable ties. Measurement consisted of recording the inter-ocular width (IO), the distance between the inside margins of the horseshoe crab's compound eyes, and the prosomal width (P), which is the distance across the horseshoe crab's carapace. Horseshoe crabs used for both bleeding mortality studies had a mean IO width of 14.0 cm and ranged from 10.5 to 19.0 cm; as well as, an average P width of 23.5 cm that ranged from 17.5 to 35.0 cm. Only animals that were uninjured (i.e., no cracked carapaces or missing legs, etc.) and free of epibionts were used in the two mortality experiments.

Experiment 1

Horseshoe crabs from the July collection were used in experiment 1. From this collection, 100 males and 100 females were selected to test only the effects of various levels of blood extraction on mortality. This sample of horseshoe crabs was termed the "lower-stressed" group because they were not exposed to external stressors associated with simulated holding and transport. The selected horseshoe crabs ranged in size to provide a representative sample of animals bled by some biomedical companies (Grogan[3]; Walls[4]). Horseshoe crabs were arbitrarily assigned to one of five bleeding treatments: 1) unbled crabs (control), 2) crabs bled 10% of their predicted total blood volume, 3) crabs bled 20% of total blood volume, 4) crabs bled 30% of total blood volume, and 5) crabs bled 40% of their predicted total blood volume. Each bleeding subgroup comprised equal numbers of males and females. Predicted blood volume was calculated by using the relationship between blood volume and IO width (Hurton et al., 2005):

$$H = 25.7e^{0.1928(IO)},$$

where H = hemolymph volume in mL; and
IO = interocular width in cm.

The bleeding process of experiment 1 involved removing horseshoe crabs from their holding tank, positioning

them in a bleeding rack, and disinfecting the surface of their arthrodial membrane with a 70% ethanol-soaked cotton swab. An 18-gauge needle was inserted through the arthrodial membrane into the cardiac sinus to extract the predetermined amount of blood. The animals were then placed in a holding container without water for 15–20 hours. Time out of water approximated the duration that horseshoe crabs may be out of water after bleeding at some biomedical bleeding facilities (Grogan[3]; Walls[4]). Bled horseshoe crabs were also not immediately put back in water to prevent them from absorbing water and regaining their blood volume. Temperatures to which horseshoe crabs were exposed were recorded using a temperature logger. Air temperature during this time was stable at 21°C. Subsequently, the animals were returned to their holding tanks and mortality was monitored for two weeks.

Experiment 2

Horseshoe crabs from the August collection were used for experiment 2. Because of difficulty in obtaining the desired 200 study animals, slightly fewer (195) horseshoe crabs were selected for this experiment. This sample of 110 males and 85 females was used to test the effects of various levels of blood extraction on mortality in the presence of external stressors. These animals represented the "higher-stressed" group because they were exposed to additional stressors to which the first group was not. The external stressors (i.e., air exposure, increased temperature, etc.) were those derived from simulated transport and holding procedures during a simulated biomedical bleeding process. Because there is great variability in transport and holding procedures and conditions, we simulated a protocol that would demonstrate horseshoe crab response under relatively poor conditions.

During the week of acclimation to the aquaculture system, the horseshoe crabs were held in the same conditions and handled in the same manner as group 1. Horseshoe crabs were assigned to one of five bleeding treatments used in experiment 1. The bleeding process of experiment 2 involved removing horseshoe crabs from their holding tank and placing them in holding containers located outside where they were exposed to air, sun, and increased temperatures. During this 6-hour period, the air temperature rose from 21°C to 29°C to simulate time on the deck of a trawler. Next, the animals were moved into a small moving truck, which was not air-conditioned. This phase simulated transportation to the bleeding facility and holding time until placement into the coldroom of the laboratory. During this 4-hour period, the outdoor temperature increased to 31°C and the temperature inside the closed truck peaked at 36°C. The animals were then transferred to the HCRC's tank room where they remained for 16 hours at 21°C. This phase mimicked the holding time in a coldroom prior to bleeding. The animals were bled according to their assigned treatment and in the same manner as in experiment 1. During this 8-hour period, the room temperature was 22°C. Once the bleeding was completed, the horseshoe crabs were moved back into the truck for 13 hours to simulate holding time and transport to the boat. The overnight temperature inside the truck dropped from 24°C to 20°C. In the morning, the horseshoe crabs were returned to the water in their recirculating aquaculture tanks and mortality was monitored for two weeks.

Statistical analyses

Fisher's exact test was used to evaluate 1) differences in mortality of unbled horseshoe crabs between the higher-stressed and lower-stressed groups, and 2) differences in mortality of bled crabs between the lower-stressed and higher-stressed groups. Logistic regression was used to examine the association between mortality and bleeding in the higher-stressed group. Data were also assessed to see if an increase in the volume bled was correlated with an increase in mortality by pooling the frequency of mortalities between males and females in each bleeding treatment and testing these values against bleeding percentage by employing a regression with a fitted quadratic curve.

Results

Experiment 1

No horseshoe crab mortality occurred in any of the five treatments in the lower-stressed group, indicating that post-bleeding mortality in *Limulus* did not arise solely from the effects of blood loss. Hence, our initial hypothesis that substantial blood loss was the principle cause of mortality in horseshoe crabs was rejected.

Experiment 2

There were a total of 14 mortalities distributed throughout the bleeding treatments among horseshoe crabs under higher stress conditions (Table 1). All mortalities occurred within the first seven days of the study. Bled horseshoe crabs had an overall mortality rate of 8.3% compared to the 2.6% mortality rate of unbled crabs, suggesting a relationship between mortality and bleeding under higher-stressed conditions (n=195; P=0.0088) (Table 1). The bleeding variable was significant in the logistic regression model (P=0.0160); yet, sex was not a significant variable (n=156; P=0.6100); seven deaths in total occurred in each sex category (Table 1). Mortality rates reached 13.6% for males bled 30% of blood volume and female mortality was as high as 29.4% in the subgroup bled 40% of blood volume (Table 1). With male and female mortalities pooled, the frequency of mortality increased as the percentage of blood taken from the crabs was increased (n=5; P=0.006; r^2=0.994) (Table 1).

Comparison of the two experiments

With no mortalities in the unbled treatment of the lower-stressed group and one mortality in the unbled treat-

Table 1

Comparison of mortalities observed in the higher-stressed group between unbled horseshoe crabs and horseshoe crabs bled at different levels of total blood volume (n=195).

	Mortality (no.)			Mortality (%)		
% bled	Male	Female	Total	Male	Female	Total
0%	1	0	1	4.5	0	2.6
10%	0	1	1	0	5.9	2.6
20%	2	0	2	9.1	0	5.1
30%	3	1	4	13.6	5.9	10.3
40%	1	5	6	4.5	29.4	15.4
Total	7	7	14	6.4	8.2	7.2

ment of the higher-stressed group, mortality rates were not significantly different between unbled crabs in the two bleeding experiments (n=79; P=0.4937). Of the bled crabs, there was a mortality rate of 0% in the lower-stressed group and a rate of 8.3% in the higher-stressed group, indicating a significant difference in mortality rates between the two groups (n=316; P<0.0001).

Discussion

According to our study of 395 horseshoe crabs, no impact on mortality was observed with blood extraction up to 40% of the horseshoe crab's blood volume under conditions of lower stressors. Any mortality associated with this maximum level of bleeding (40% of total blood volume) was so low that it was not captured by our sample size of 40 individuals per bleeding treatment. This result also may indicate that despite hypovolemia, or low blood volume, and altered blood chemistry (Hurton, 2003), horseshoe crabs may be relatively tolerant of the removal of a large amount of blood in the absence of other stressors.

Horseshoe crab mortality, however, was significant in the presence of higher levels of stress, including external stressors (i.e., lengthy air exposure, elevated temperatures, etc.) as applied in our study. Novitsky's (1991) aquarium studies reported that up to 30% of blood volume can be safely extracted, indicating that the animals in that study may have been similar to our lower-stress group; however, details regarding harvest method, transport, and handling procedures were not specified (Novitsky, 1991). It is likely that, under different conditions, horseshoe crab response to blood extraction may be altered. Findings from our study indicated that a combination of external effects and sublethal hemorrhaging may result in significantly increased mortalities, possibly from a synergistic interaction between the two types of stressors. Studies in other species exposed to various stressors have also indicated that mortality may be affected by a synergistic combination of effects from multiple stressors (Schisler et al., 2000; Schulz and Dabrowski, 2001; Hatch and Blaustein, 2003). Such results emphasize the importance of considering the cumulative impact of multiple stressors.

Although the data in our study indicated a significantly increased mortality rate in the higher-stressed group as opposed to the lower-stressed group, it is important to note the variability in mortality throughout the treatments. It was observed that the male and female horseshoe crabs had different and variable responses in the different bleeding treatments. For example, males had two and three mortalities in the 20% and 30% bleeding treatments, respectively; yet, only one mortality in the 40% treatment (Table 1). Females appeared to have a spike in mortality in the 40% treatment (Table 1). When viewing the data this way, the variability in mortality could be in part due to the health and precollection stress level of a horseshoe crab, which can differ from its counterparts. Different conditions may lead to different responses and not every individual will react exactly alike. More than likely, much of this variability is an artifact of a small sample size. Once the male and female data were pooled, total mortality appeared to proceed in an increasing trend as bleeding amount increased (Table 1). If sample size were increased enough, perhaps a strong trend would emerge in mortality between males and females, or perhaps not. Further investigation with larger sample sizes and a different experimental design could shed light on a possible trend in male and female mortality rates and whether one sex may be more susceptible to mortality than the other.

The combination of multiple stressors could also affect not only mortality, but possibly the amount of blood able to be extracted by the biomedical industry. It is possible that horseshoe crabs exposed to higher levels of external stress, such as greater lengths of time to air and higher temperatures, would lose moisture from their exposed gills and possibly become dehydrated and thus have a decreased blood volume such that a smaller amount of blood is available for extraction. It is unknown how this would affect the harvest of horseshoe crab blood for the production of LAL. Dehydration rates in horseshoe crabs are unknown, but have been examined in a freshwater crayfish (*Austropotamobius pallipes*) which is a facultative air breather that can survive about three days out of water (Taylor et al., 1987). Taylor et al. reported that when exposed to air (70–80% relative humidity) for 27 hours, crayfish became dehydrated and had a 25% decreased blood volume. When exposed to water-saturated air (100% relative humidity), crayfish did not have a decrease in blood volume. Similarly, horseshoe crabs exposed to water-saturated air may be less likely to become dehydrated, thereby possibly decreasing the effects of one type of stress.

The results presented in the present study provide insight into the possible combined effects of blood extraction and external stressors associated with biomedical

transport and holding methods on horseshoe crab mortality. Of the various protocols followed in the bleeding process, we simulated an example of transport, holding, and bleeding methods that provided poor conditions for the horseshoe crabs and that resulted in significant mortality rates. In the typical biomedical bleeding process, horseshoe crabs undergo time on a boat deck or in collection bins, transport, storage in a coldroom, bleeding, holding time, and transport back to the ocean. At each of these stages of processing, the animals are exposed to a number of stressors of varying magnitudes, including exposure to air for extended time periods, elevated temperatures, dehydration, hypovolemia, and likely other unknown stressors. However, these factors can be controlled to a certain extent by providing conditions for the horseshoe crabs that could alleviate much of the stress. For example, holding horseshoe crabs in an air-conditioned environment (i.e., during time in the truck and in the cold room), covering the animals with wet burlap while outside to keep them moist and shaded from the sun, and increasing the relative humidity of the air in the holding room could help to decrease the physiological stress the animals experience throughout the bleeding process. Because blood volume estimates have recently been determined (Hurton et al., 2005), the blood volume extracted by biomedical companies potentially could be optimized according to average stress conditions and attempts could be made to decrease stress as much as feasibly possible, including keeping horseshoe crabs hydrated and bleeding a prescribed amount from individuals, as opposed to withdrawing a wide range of blood volumes. Another important consideration is stress arising from harvest methods. Our study did not test the effects of this factor, but it may have an effect on the condition of horseshoe crabs collected for bleeding. Biomedical companies should include the potential effects of harvest methods when determining what may be typical stressful conditions for the horseshoe crabs, or they could consider using a harvesting method that would be the least stressful on the animals. All LAL producers can potentially implement some form of these recommendations, thereby altering bleeding process protocols to decrease the stress and mortality levels that these horseshoe crabs experience. Implementation of these recommendations would decrease the impact of the biomedical industry on the potentially declining horseshoe crab population and aid in conservation of this species.

Acknowledgments

This work is a result of research sponsored in part by the NOAA Office of Sea Grant, U.S. Department of Commerce, under Grant no. NA96RG0025 to the Virginia Graduate Marine Science Consortium and Virginia Sea Grant College Program. Cambrex Bio Science Walkersville, Inc. generously supplied us with horseshoe crabs for the study. We wish to thank Stephen Smith of the Virginia-Maryland College of Veterinary Medicine at Virginia Tech for his help in the planning of this study. We also thank Eric Hallerman of the Department of Fisheries and Wildlife Sciences of Virginia Tech for his helpful comments throughout this project. In addition, Xin Zhong and Li Wang of the Department of Statistics at Virginia Polytechnic Institute and State University were the statistical consultants for this project. We offer a special thanks to numerous colleagues for their assistance in transporting, tagging, and bleeding horseshoe crabs for this study. We greatly appreciate the time and effort of all involved.

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A study of tagging methods for the sea cucumber *Cucumaria frondosa* in the waters off Maine

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The sea cucumber fishery in waters off Maine is developing and has recently experienced great increases in landings, corresponding to expanding export markets. Between 1994 and 1996, reported landings ranged from one to three million pounds (Fig. 1). In 1999, reported landings were over eight million pounds and rose to over nine million in 2000 (Feindel[1]). Like other developing fisheries, we have little information about the biology and ecology of the sea cucumber off Maine, limited data on the fishery, and little knowledge about the key life history processes that characterize its population dynamics. Therefore, we have a limited understanding of the current status of the resource and the impacts the fishery may have on the stock.

Most research done so far has been done on the red sea cucumber (*Parastichopus californicus*) in the northwestern United States and British Columbia (e.g., Bradbury et al., 1996; Zhou and Shirley, 1996; Phillips and Boutillier, 1998; Perry et al., 1999; Cripps and Campbell, 2000). Limited research has been done along the eastern coast of North America, although some studies have added to our knowledge of *Cucumaria frondosa*. A study of the ecology and behavior of *C. frondosa* was conducted in Maine by Jordan (1972). More recent studies have focused on fertilization success and feeding behavior as it relates to aquaculture (Hamel and Mercier, 1997; Medeiros-Bergen and Miles, 1997; Singh et al., 1998). These studies have improved our knowledge of *C. frondosa* but still do not provide enough information on growth, one of the life history processes most important for understanding the population dynamics of sea cucumbers in waters off Maine.

Because of the lack of hard tissue in sea cucumbers to lay down growth increments, tagging is the method undertaken to determine age. Tagging studies of sea cucumbers are difficult because external tags are frequently lost and internal tags can be shed through the body wall. Sea cucumbers have been tagged *in situ* with limited success (Shelley, 1981; Conand[2]) by using a small T-bar tag that is inserted through the body wall with a tagging gun (Harriott, 1980). Previous studies of manual tags in *P. californicus* in Washington indicated that the presence of these tags had no significant effect on the behavior of the sea cucumbers and did not affect their ability to react to shifts in the salinity of the experimental medium (Fankboner[3]). Typically, necrosis of the tissue surrounding the tag occurs and tags fall out within a few months (Morgan, 2000). Morgan suggested that this method may be adequate for tagging broodstock in captivity over short periods of time and stated that tag loss may be minimized by ensuring that the T-bar is pushed right through the dermis and attempting to make a puncture wound that is as small and clean as possible. Schroeter et al. (2001) used tags to conduct a growth study of *P. parvimensis* in California by following individuals through repeated surveys at two sites. Only 17.6 % of 1224 tagged animals were recaptured over one year. These studies indicate that manual tags may not be an effective means for studying growth because of the high frequency of shedding tags by sea cucumbers.

Previous researchers have also used fluorescent dyes to stain the calcareous plates surrounding the buccal cavity of sea cucumbers but with varied results. Successful staining has depended on the timing of the injection of the dye and the deposition of calcium for growth of the mouthparts (Conand[2]). Other work has suggested that fluorescent marking by dyeing the ossicle of the juveniles with tetracycline may be useful (Tanaka[4]). However, injec-

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Manuscript submitted 13 October 2004 to the Scientific Editor's Office.

Manuscript approved for publication 26 July 2005 by the Scientific Editor.

Fish. Bull. 104:299–302 (2006).

tions are time-intensive and marks often become difficult to discern after several months. Also, sea cucumbers could not be located soon after release in some follow-up investigations.

Yanagisawa (1995) successfully used a hot wire to brand the sea cucumber *Stichopus japonicus*. Although most of the marked juveniles could be distinguished three months later, it seemed to be difficult to discern their marks after four months.

The results of previous worldwide sea cucumber tagging studies vary in success by species, investigator, and location. It is also possible that the technique varied significantly for studies involving the same styles of tagging. Therefore, the conclusions of these previous tagging studies may not be applied to the sea cucumber population off Maine. Factors such as dermal thickness and seasonal fluctuations likely alter the capacity of the sea cumcumber to retain tags.

The objective of this study was to ascertain whether a reliable means of tagging the Maine sea cucumber could be identified. Tagged animals would provide information on growth and movement for later studies. This important biological information would be critical for sea cucumber stock assessment and management.

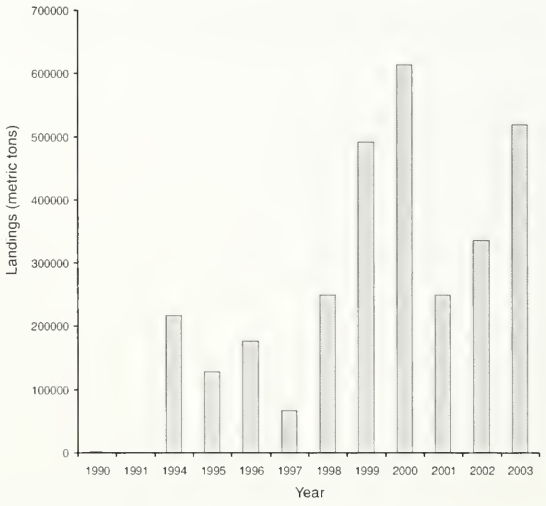

Figure 1

Historical landings (metric tons) for the sea cucumber *Cucumaria frondosa* fishery in Maine.

Materials and methods

The study was carried out between April and September 2003 to determine the effectiveness of various tags. Initially, animals were tested by using 1) long and short double T-bar tags inserted with a tagging gun; 2) dart tags; 3) streamer tags; and 4) cinch-up tags. A control group was also included in which animals were punctured with the tagging gun to observe any mortality from the piercing. It was evident in the first minute that dart tags, streamer tags, and cinch-up tags would not stay within the cucumber body wall and these methods were not considered further.

Next, 5) a rope gun was tested as a means of scarring (branding) animals. Rope guns are normally used to burn through rope by applying the hot tip to the surface of a rope. For tagging purposes, the rope gun tip was applied to the dermis of *C. frondosas* to produce a recognizable scar; the process is similar to that used in branding cattle. Although the rope gun created a noticeable mark, many animals already possessed significant scarring from being dragged during harvesting or from interactions with fishing gear and other marine organisms, and the new scar would not stand out to an observer. The branding method was therefore also discarded.

Finally, 6) liquid orange and yellow fluorescent dyes composed of visible implant elastomer (VIE) were injected into the animals. VIE is a silicone-based material that is mixed immediately before use and quickly becomes a pliable, biocompatible solid. VIE tags were injected internally beneath the epidermal tissue within tube feet, along the body wall, or near the oral cavity. The dye did not spread and all marks were small pin points visible only under ultraviolet light.

Short and long double T-bar tags and fluorescent dyes served as the remaining tagging methods studied during the course of the investigation. Seventy tagged sea cucumbers from the Gulf of Maine were observed over time (Table 1). Ten animals were injected with orange and yellow fluorescent dyes and 45 animals were punctured with long or short T-bar tags. Long tags had a distance of 45 mm between T-bar ends. Short tags had a distance of 19 mm between T-bar ends. Twenty-one tags punctured the body wall just under the muscle so that one end remained inside the animal (single-anchor tags). The remaining 24 passed completely through the body wall twice so that both ends of the T-bar tags were exposed (double-pass tags). Finally, 15 control animals were punctured with the tagging gun, 9 with double punctures and 6 with single punctures. Sea cucumbers were kept in tanks in the laboratories at the Maine Department of Marine Resources in West Boothbay Harbor, Maine. The presence and absence of tags was noted every day from April to September 2003 for each sample. Notation was made when tags were partially in place or no longer observable at all.

Results and discussion

Table 1

Tagging study design for the sea cucumber *Cucumaria frondosa* off Maine. Total numbers sampled for each method are indicated as total animals in the right column. Parentheses identify the number of animals sampled.

Tagging method				Total animals
Fluorescent dyes				10
Double T-bar tags				
Double-pass	Single-anchor			45
Long tag (9)	Long tag (6)			
Short tag (15)	Short tag (15)			
Control				15
Tagging gun puncture	Double-puncture (9)	Single-puncture (6)		
Total				70

The tagging study was successful in providing information on retention rates for the different tagging methods observed during the 140 days of the investigation (Fig. 2). Fluorescent dye injections and single-anchor long T-bar tags were the most successful means identified in tagging sea cucumber in the waters off Maine. Eighty percent with dye continued to fluoresce under the UV light and 65% of single-anchor long T-bar tags remained embedded in the sea cucumbers at the end of the investigation on day 140. The T-bar method may be the most practical for short-term research on this species considering the time and expense of fluorescent dye injection. Another advantage over injections is that the tagging gun technique is much more easily repeatable among subjects, whereas the site of injection varied among animals depending on the location of soft tissue.

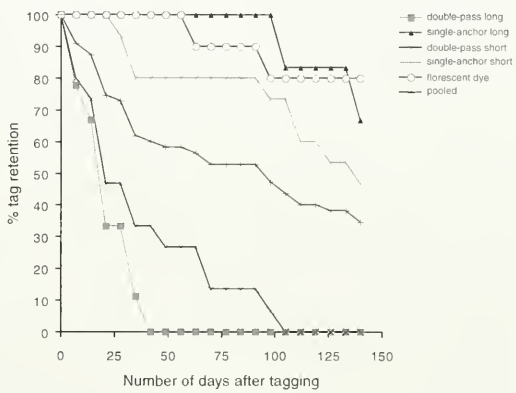

Figure 2

Tagging retention in the sea cucumber *Cucumaria frondosa* for individual-style tags over 140 days of observation in the waters off Maine. Note that florescent dye and single-anchor long T-bar tags were the most successful methods identified.

Double-pass T-bar tags were expelled faster than those in the single-anchor condition. With the double-pass tag, it appeared that the long portion of the tag under the animal's epidermis gradually moved upward until it was expelled outside of the skin without scarring the animal. The longer bars were pushed out the fastest and all were shed before day 50. Shorter T-bar tags took almost twice as long to reach 0% retention as the longer T-bars in the double-pass condition, perhaps because the shorter bars pinched the dermis tightly between tag bars, whereas animals with the longer bars were able to relax their entire body wall. After tags were shed in all T-bar conditions, it was not possible to tell which experimental condition each individual had experienced. No mortality was observed from the tags or from the control punctures.

Five T-bar tagged animals experienced a punctured respiratory tree caused by the tagging gun. The respiratory tree is an internal organ used for breathing by pumping seawater in and out. After the initial puncture, no trace of the injury could be detected and no differences in appearance or behavior were noted throughout the investigation. Although it was not possible to track which individuals had a partially punctured respiratory tree, injured individuals may have shed tags at a different rate than others in their cohorts. Internal injuries may also have affected the results of later studies of growth and movement with the use of manual tags. With the use of a largest possible sample size and careful placement of the tagging gun, this potential bias can be minimized. Additionally, it is important to consider that tag retention rate in the field may vary more than results observed in the laboratory.

We believe that the fluorescent dye injections and single-anchor long-T-bar tagging methods in our investigation will likely prove effective for a longer-term study with additional preliminary tagging analysis. However, a more effective way to study the growth of sea cucumbers may be the combination of caging and tagging, where tagged individuals of similar size are put in the same cage to monitor a change in size.

Future investigations will test different locations for, and methods of, injecting fluorescent dye and single-anchor long T-bar tags and will help to further identify the best tagging method. When the most successful method is determined, a long-term study will allow us to understand how individual animals grow, move, and change both seasonally and annually.

Acknowledgments

The Northeast Consortium, Maine Sea Grant, and Maine Department of Marine Resources provided funding. Kirshenbaum was supported by a fellowship from the Kendall Foundation.

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Parameterizing probabilities for estimating age-composition distributions for mixture models

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When estimating parameters that constitute a discrete probability distribution $\{p_j\}$, it is difficult to determine how constraints should be made to guarantee that the estimated parameters $\{\hat{p}_j\}$ constitute a probability distribution (i.e., $\hat{p}_j>0$, $\Sigma\hat{p}_j=1$). For age distributions estimated from mixtures of length-at-age distributions, the EM (expectation-maximization) algorithm (Hasselblad, 1966; Hoenig and Heisey, 1987; Kimura and Chikuni, 1987), restricted least squares (Clark, 1981), and weak quasisolutions (Troynikov, 2004) have all been used. Each of these methods appears to guarantee that the estimated distribution will be a true probability distribution with all categories greater than or equal to zero and with individual probabilities that sum to one. In addition, all these methods appear to provide a theoretical basis for solutions that will be either maximum-likelihood estimates or at least convergent to a probability distribution.

However, all these methods are presented in a theoretical context that is useful in understanding the theory, but may not be suitable for actual application. Currently, most modelers will have an optimization program available. This note describes how, in a brief amount of time, the modeler can add a mixture model program to his collection of readily available programs—one that will estimate maximum-likelihood estimates for the mixture problem and will incorporate the experimenter's familiar optimization program.

To do this it is necessary to parameterize the estimated probabilities so that they are in fact guaranteed to constitute a probability distribution (i.e., $\hat{p}_j>0$, $\Sigma\hat{p}_j=1$). Two such parameterizations are the multinomial logit and a parameterization method described by Heifetz and Fujioka (1991). The trick with both parameterizations is that although the parameters that are actually estimated are unconstrained, these unconstrained estimates can be easily transformed to constrained probability estimates.

Materials and methods

Multinomial logit parameterization

Consider parameterizing the probabilities using the classic logit model:

$$p_j = \frac{r_j}{(1+\sum r_k)} \quad j,k=1,\ldots,a-1 \text{ and}$$

$$p_a = \frac{1}{(1+\sum r_k)}.$$

The r_j can be guaranteed to be positive by defining $r_j=\exp(x_j)$. The parameters that are estimated are $x_j=\ln(r_j)$. In turn the $\{x_j\}$ are used to estimate the $\{r_j\}$, and then the $\{p_j\}$. Thus, $x_1, \ldots, x_{a-1}$ if are estimated on $(-\infty, \infty)$, the resulting $\{\hat{p}_j\}$ is guaranteed to be a probability distribution. The relationship between the $\{p_j\}$ and $\{r_j\}$ is a unique one-to-one mapping because given any $\{p_j\}$, $r_j=p_j/p_a$, for $j=1, \ldots, a-1$.

Heifetz and Fujioka parameterization

Heifetz and Fujioka (1991), for a tagged fish migration problem, used a somewhat similar parameterization that guaranteed estimated parameters would be probability distributions. Suppose a distribution consisted of categories with probabilities $\{p_j\}$. The Heifetz-Fujioka (H-F) parameterization would be

$$p_j = \frac{r_j}{\sum r_k}\left(1-\exp(-\sum r_k)\right)$$

$$j,k=1,\ldots,a-1 \text{ and}$$

$$p_a = \exp(-\sum r_k)$$

$$\text{where } r_k>0 \text{ for } k=1,\ldots,a-1.$$

As above r_j, can be guaranteed to be positive by defining $r_j=\exp(x_j)$ and the parameters that are estimated are $x_j=\ln(r_j)$. Also as above, $\{x_j\}$ are used to estimate the $\{r_j\}$, and then the $\{p_j\}$. Thus, if $x_1, \ldots, x_{a-1}$ are estimated on $(-\infty, \infty)$, the resulting $\{\hat{p}_j\}$ is guaranteed to be a probability distribution. The relationship between the $\{p_j\}$ and $\{r_j\}$ is a unique one-to-one mapping because given any $\{p_j\}$, $r_j=-p_j\ln(p_a)/(1-p_a)$, for $j=1, \ldots, a-1$.

H-F probabilities as exploitation rates

Stock assessment modelers would recognize the formula

$$p_j = \frac{r_j}{\sum r_k}\left(1-\exp(-\sum r_k)\right)$$

as the exploitation rate formula where p_j takes the role of the exploitation rate (u_j) and r_j takes the role of the instantaneous mortality rate F_j. The formula $r_j=-p_j\ln(p_a)/(1-p_a)$ indicates that the instantaneous mortality rate can be solved in closed form, but this is generally not true because the natural mortality rate M is generally known as an instantaneous mortality rate rather than an exploitation rate.

Manuscript submitted 20 January 2005 to the Scientific Editor's Office.

Manuscript approved for publication 2 August 2005 by the Scientific Editor.

Fish. Bull. 104:303–305 (2006).

However, when exploitation rates are all known, as in some ecological modeling exercises (e.g., $u_j=C_j/N_j$, i.e., catch per population), then all instantaneous mortality rates can be solved in closed form.

Example: As an example, the logit and H-F parameterization can be used to estimate the distribution mixture problem for empirical length-at-age data. To describe the mixture problem for empirical length-at-age data, let

$i = 1, \ldots, n$ be the length category index;
$j = 1, \ldots, a$ be the age category index;

f_i = the observed length frequency, for which we wish to estimate the corresponding age distribution;
$\bar{f}_i = f_i/f$, where $f=\Sigma f_i$, the observed length distribution;
p_j = the unknown age distribution we wish to estimate from the observed length distribution;
q_{ij}=Prob[$i|j$] = the observed distribution of length at age, estimated from age-length data;
$l_i = \Sigma_j p_j q_{ij}$ = length distribution estimated from an age distribution and observed length-at-age distributions.

Solutions to the empirical distribution mixture problem can be stated as solving for that age distribution $\{p_j\}$, which when combined with length i at age j, say $\{q_{ij}\}$, provides the "best" weighting to reproduce some length frequency $\{\bar{f}_i\}$. "Best" may be defined as

1 Maximum likelihood (Kimura and Chikuni, 1987):

$$L = const. + \sum_{i=1}^{n} f_i \log(l_i).$$

2 Minimum chi-square

$$\chi^2 = \sum_{i=1}^{n} (f_i - f l_i)^2 / (f l_i).$$

For both of these estimation problems, the estimated $\{\hat{p}_j\}$ distribution must be constrained to sum to one. The logit or H-F parameterization simplifies and unifies the estimation of $\{p_j\}$ for these or any other objective function. Any multivariate function optimization program, using these parameterizations, can generate estimated probability distributions whose components are positive and will be guaranteed to sum to one. Therefore any multivariate optimization program with these parameterizations can be used to estimate $\{p_j\}$.

Results

Greenland turbot (*Reinhardtius hippoglossoides*) length-at-age data were originally used to illustrate the iterated age-length key (IALK) (Kimura and Chikuni, 1987).

Table 1

Age distributions for Greenland turbot (*Reinhardtius hippoglossoides*) estimated by fitting length at age data to 1983 length-frequency data (Kimura and Chikuni, 1987). Except for the iterated age-length key (IALK) algorithm, all estimates were arrived at by using the logit or Heifetz-Fujioka (H-F) parameterizations which provided identical results.

Age (yr)	Maximum likelihood	IALK algorithm	Minimum χ^2
4	0.0353	0.0353	0.0377
5	0.1903	0.1903	0.1858
6	0.2281	0.2281	0.2229
7	0.1291	0.1291	0.1318
8	0.1125	0.1125	0.1117
9	0.0380	0.0380	0.0349
10	0.0525	0.0525	0.0554
11	0.0000	0.0000	0.0000
12	0.0332	0.0332	0.0383
13	0.0023	0.0023	0.0000
14	0.0204	0.0204	0.0235
15	0.0168	0.0168	0.0162
16	0.0289	0.0289	0.0248
17	0.0253	0.0253	0.0218
18	0.0680	0.0680	0.0719
19	0.0042	0.0042	0.0036
20	0.0152	0.0152	0.0198

We used the 1983 length-frequency data from that data set, along with the length-at-age data, to illustrate the methods of estimating mixture probabilities with the logit and H-F parameterizations (Table 1). Except for results from the IALK algorithm, all parameters were estimated by using an optimization program with the logit and H-F parameterizations (i.e., the latter two parameterizations gave identical results). Results also showed that maximum-likelihood estimates from either the logit or H-F parameterizations provided maximum-likelihood estimates identical to those estimated by using the IALK algorithm.

Discussion

It is probable that the logit and H-F parameterizations would provide nearly identical solutions for a given data set and objective function. If maximum likelihood solutions are unique, either parameterization should provide the maximum-likelihood estimates because the reparameterizations of probabilities are one-one mappings that lead to invariance properties when optimization is performed. The maximum-likelihood solutions will generally be unique when all $\hat{p}_j>0$ (Kimura and Chikuni, 1987). However, difficulties in searching in multivariate spaces, and limited computational precision may cause differences in the estimates.

Simple parameterizations, like direct estimates of $\{p_j\}$, will allow solutions that have negative probabilities. Constrained solutions, which allow maximum likelihood estimates and other types of estimates, will generally make these negative components of the probability distribution have zero values. Such solutions are boundary value solutions and may not be unique (Kimura and Chikuni, 1987). This is another reason it is difficult to claim unique solutions for the mixture problem.

From the modeling perspective, we illustrate the usefulness of reparameterization to impose mathematical constraints. In the context of the mixture problem the suggested parameterizations are reasonably transparent and allow the modeler to use familiar software. The reason we propose the methods described in this note is not that these methods provide superior estimates to those described in the literature, but that the procedure for estimation may actually be more straightforward and transparent for modelers more interested in solutions than in theory.

Because of its simplicity, effectiveness, and ready applicability to different objective functions, modelers may prefer optimization using the logit or H-F parameterizations to estimate probability distributions for the mixture problem. Another advantage of these reparameterizations is that they can be more generally applied, for example, to estimate geographic distribution in migration models (Heifetz and Fujioka, 1991; Shimada and Kimura, 1994).

Acknowledgments

We thank two anonymous referees for comments that helped us clarify our presentation.

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Morphometric differentiation in small juveniles of the pink spotted shrimp (*Farfantepenaeus brasiliensis*) and the southern pink shrimp (*F. notialis*) in the Yucatan Peninsula, Mexico

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The morphometric and morphological characters of the rostrum have been widely used to identify penaeid shrimp species (Heales et al., 1985; Dall et al., 1990; Pendrey et al., 1999). In this setting, one of the constraints in studies of penaeid shrimp populations has been the uncertainty in the identification of early life history stages, especially in coastal nursery habitats, where recruits and juveniles dominate the population (Dall et al., 1990; Pérez-Castañeda and Defeo, 2001). In the western Atlantic Ocean, Pérez-Farfante (1969, 1970, 1971a) described diagnostic characters of the genus *Farfantepenaeus* that allowed identification of individuals in the range of 8–20 mm CL (carapace length) on the basis of the following morphological features: 1) changes in the structure of the petasma and thelycum; 2) absence or presence of distomarginal spines in the ventral costa of the petasma; 3) the ratio between the keel height and the sulcus width of the sixth abdominal somite; 4) the shape and position of the rostrum with respect to the segments and flagellum of the antennule; and 5) the ratio between rostrum length (RL) and carapace length (RL/CL). In addition, she classified *Farfantepenaeus* into two groups according to the shape and position of the rostrum with respect to the segments and flagellum of the antennule and the ratio RL/CL: 1) *F. duorarum* and *F. notialis*: short rostrum, straight distally, and the proximodorsal margin convex, usually extending anteriorly to the end of distal antennular segment, sometimes reaching to proximal one-fourth of broadened portion of lateral antennular flagellum, with RL/CL <0.75; and 2) *F. aztecus*, *F. brasiliensis*, *F. paulensis*, and *F. subtilis*: long rostrum, usually almost straight along the entire length, extending anteriorly beyond the distal antennular segment, sometimes reaching to the distal one-third of broadened portion of lateral antennular flagellum, with RL/CL >0.80. Pérez-Farfante stressed that, for the recognition to species level of juveniles <10 mm CL, all the characters listed above should be considered because occasionally one alone may not prove to be diagnostic. However, the only characters that could be distinguished for small juveniles in the range 4–8 mm CL are those defined on the rostrum. Therefore, it has been almost impossible to identify and separate small specimens of *Farfantepenaeus* (Pérez-Farfante, 1970, 1971a; Pérez-Farfante and Kensley, 1997).

Pink spotted shrimp (*F. brasiliensis*) and southern pink shrimp (*F. notialis*) have a wide geographic distribution in coastal environments of the Atlantic Ocean. The pink spotted shrimp is distributed within the western Atlantic from Cape Hatteras, North Carolina, to Cabo Frio, Brazil (22°00′S, 42°00′W: Pérez-Farfante, 1969), including the southwestern Gulf of Mexico and the Caribbean coasts of Mexico (Pérez-Farfante, 1971b). The southern pink shrimp ranges from the northwestern Yucatan Peninsula, Mexico (20°45′N, 90°25′W: Pérez-Castañeda and Defeo, 2000), to Rio de Janeiro (Brazil) in the western Atlantic, including Cuba and the Virgin Islands in the Caribbean Sea. The species is also reported from Mauritania to Angola in the eastern Atlantic Ocean (Pérez-Farfante, 1969; Pérez-Farfante and Kensley, 1997).

The current identification keys show that, for shrimps ≥8 mm CL, the pink spotted shrimp has a proportionately longer rostrum than the southern pink shrimp. However, there are no scientific data to separate these species at individual sizes <8 mm CL (Pérez-Farfante, 1970, 1971a). This is particularly important where both penaeid shrimps are found in the same region, mainly between the Yucatan Peninsula and along the Caribbean coast of Mexico, Puerto Rico, and Colombia. In this geographic region, small juveniles of both species have been almost impossible to separate and have been classified only to genus level (Stoner and Zimmerman, 1998; May-Kú, 1999; Pérez-Castañeda and Defeo, 2001; Criales et al., 2002). In this note we provide quantitative and qualitative information that allows separation of the sympatric *F. brasiliensis* and *F. notialis* in the range of 4–8 mm CL based on shrimp collected in the Río Lagartos and Yalahau coastal lagoons of the Yucatan Peninsula, Mexico.

Materials and methods

Shrimp were collected by using a Renfro beam trawl (1.6×0.5 m mouth, 1.5 m total length, and 1.0-mm mesh), which was hand hauled in two coastal lagoons of northeastern Yucatan Peninsula (Fig. 1). The Río Lagartos

Manuscript submitted 8 March 2005
to the Scientific Editor's Office.
Manuscript approved for publication
22 August 2005 by the Scientific Editor.
Fish. Bull. 104:306–310

lagoon (21°26′–21°38′N, 87°30′–88°15′W) was sampled from November 1996 to April 1997, whereas the Yalahau lagoon (21°26′–21°36′N, 87°08′–87°29′W) was sampled from June 2001 to May 2002. These coastal lagoons are considered the main nursery areas for *F. brasiliensis*, accounting for 80–95% of the total shrimp abundance, followed by *F. notialis* (May-Kú, 1999; May-Kú and Ordóñez-López, 2000). Shrimps (4–10 mm CL) were preserved in 10% formaldehyde, prior to examination. Rostrum length (RL; distance from the tip of the rostrum to the postorbital margin of the carapace) and carapace length (CL; distance from the postorbital margin to the posterior margin of the carapace) were measured with an ocular micrometer to the nearest 0.1 mm. Furthermore, the shape and position of the rostrum with respect to the segments and flagellum of the antennule were considered (Pérez-Farfante, 1969; 1970, 1971a). Shrimps ranging from 8 to 10 mm CL were identified to species level according to the characters outlined by Pérez-Farfante (1970, 1971a). The relationship between rostrum length and carapace length (RL-CL) was determined for each species (*F. brasiliensis*, *F. notialis*) in each lagoon, and fitted to the linear function $RL = a + b\ CL$, where a and b are coefficients. One-way analysis of covariance (ANCOVA) was used to evaluate differences between species in the RL-CL relationship for each site, with RL as the dependent variable and CL as the covariate. Assumptions of homoscedasticity and homogeneity of slopes (parallelism) were met after log-transformation of RL. Lastly, the RL/CL ratio was estimated to remove the differences in individual sizes between species, then plotted against CL and determined for each lagoon. A one-way analysis of variance (ANOVA) was conducted to test interspecific differences between mean RL/CL in each lagoon. The original RL/CL values were log-transformed to fulfill ANOVA assumptions.

Results

A total of 13,234 shrimps in the size range 4–10 mm CL were collected. Of the 727 organisms measured in the Río Lagartos lagoon, 74.6% were *F. brasiliensis* and 25.4% *F. notialis*. In Yalahau lagoon, from the 12,507 organisms measured, 91.7% were *F. brasiliensis* and 8.3% *F. notialis*. In the two lagoons, both species showed a significant positive linear RL-CL relationship ($r^2 \geq 0.92$; $P<0.001$). Significant differences were detected between the species (ANCOVA: $P<0.001$; Fig. 2; Table 1)—*F. brasiliensis* having a longer rostrum than *F. notialis* for a given CL.

The RL/CL ratio for both species ranged from 0.42 to 0.94. In both lagoons the scatter plots

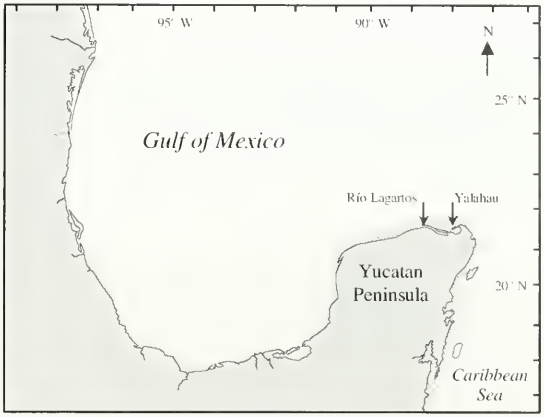

Figure 1

Location of Río Lagartos and Yalahau lagoons off the Yucatan Peninsula. The distribution of *Farfantepenaeus brasiliensis* and *F. notialis* along the Mexican coast of the Gulf of Mexico and Caribbean Sea is indicated by oblique lines.

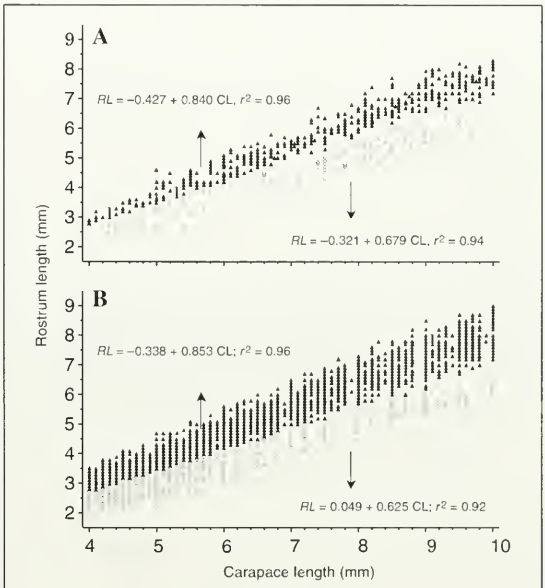

Figure 2

Relationships between rostrum length (RL) and carapace length (CL) fitted by the linear model $RL = a + b\ CL$ for juveniles of *Farfantepenaeus brasiliensis* (▲) and *F. notialis* (◇) from (**A**) Río Lagartos and (**B**) Yalahau lagoons. All regressions are highly significant ($P<0.001$).

Table 1

Parameters of the linear regression model between rostrum length (RL) and carapace length (CL) fitted for *Farfantepenaeus brasiliensis* and *F. notialis*, in the size range of 4–10 mm CL, for Río Lagartos and Yalahau. ANCOVA results (log-transformed RL) are also shown, including tests of homogeneity of slopes and differences in RL at CL (main effect) between species. "*a*" and "*b*" represent, respectively, the intercept and slope of the regression lines. SE = standard error; ns = not significant; *** = $P<0.001$.

	a Mean (SE)	*b* Mean (SE)	r^2	*n*	*P*
Río Lagartos					
F. brasiliensis	−0.427 (0.055)***	0.840 (0.007)***	0.96	542	***
F. notialis	−0.321 (0.091)***	0.679 (0.013)***	0.94	185	***
ANCOVA					
Homogeneity of slopes: $F_{1,723}$=1.212; P=0.271					
Main effect: $F_{1,724}$=1,430.2; P=0.00001					
Yalahau					
F. brasiliensis	−0.338 (0.010)***	0.853 (0.002)***	0.96	11,467	***
F. notialis	0.049 (0.032) ns	0.625 (0.006)***	0.92	1040	***
ANCOVA					
Homogeneity of slopes: $F_{1,12503}$=0.966; P=0.326					
Main effect: $F_{1,12504}$=12486.4; P=0.0001					

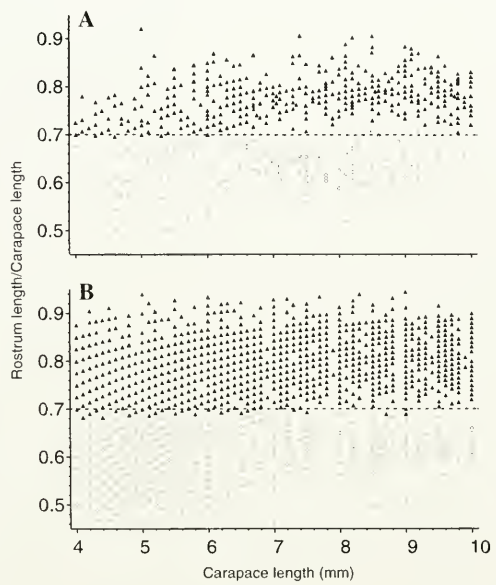

Figure 3

Scatter plot of rostrum length/carapace length (RL/CL) ratios against CL for juveniles of *Farfantepenaeus brasiliensis* (▲) and *F. notialis* (◊) from (**A**) Río Lagartos and (**B**) Yalahau lagoons. The separation between species at RL/CL = 0.70 is indicated by a dotted line.

of RL/CL ratios against CL by species fell into two distinct clouds representing dissimilar morphometric characteristics of the species, with the point of separation between species set at a value of 0.70 (Fig. 3). The RL/CL ratios were significantly higher in *F. brasiliensis* than in *F. notialis*, both for Río Lagartos (ANOVA, $F_{1,725}$=1778.33, $P<0.001$) and Yalahau (ANOVA $F_{1,12505}$=16627.64, $P<0.001$). For Río Lagartos, *F. brasiliensis* had a mean RL/CL ratio ±SD of 0.78 ±0.04 and a range of 0.70–0.92, whereas the mean RL/CL ratio in *F. notialis* was 0.63 ±0.04, with a range of 0.50–0.72. In Yalahau lagoon, the RL/CL ratio in *F. brasiliensis* was 0.80 ±0.05 (range 0.68–0.94), whereas in *F. notialis* these values were 0.62 ±0.05 (0.43–0.69; Fig. 4). The above values indicate a morphometric divergence between the two species, with higher values corresponding to *F. brasiliensis* and lower ones to *F. notialis*.

Small juveniles presented clear differences between species in the shape and position of the rostrum with respect to the segments and the flagellum of the antennule. *Farfantepeaeus brasiliensis* had a rostrum that was straight and slender, extending beyond the 3rd antennular segment, and generally reaching the broadened portion of lateral flagellum (Fig. 5A), whereas *F. notialis* had a lightly convex rostrum, never extending beyond the third antennular segment (Fig. 5B).

Discussion

We found clear morphometrical and morphological rostrum differences between small juveniles

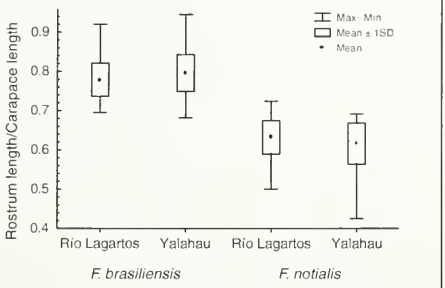

Figure 4

Box and whisker plots of the rostrum length/carapace length (RL/CL) ratios for *Farfantepenaeus brasiliensis* and *F. notialis*, discriminated by lagoon.

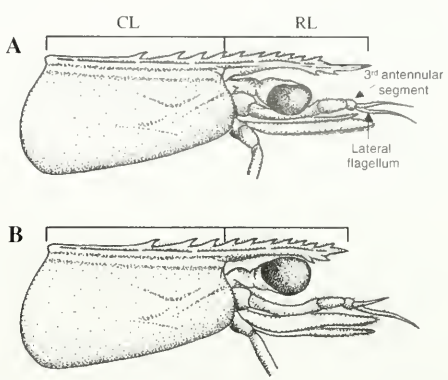

Figure 5

Distinguishing features of the shape of the rostrum and its position with respect to the segments and the flagellum of the antennule in *Farfantepenaeus brasiliensis* (**A**) and *F. notialis* (**B**). CL = carapace length, RL = rostrum length.

(4–8 mm CL) of *F. brasiliensis* and *F. notialis* in two coastal lagoons of the Gulf of Mexico. Our results also complement those obtained by Pérez-Farfante (1969; 1970, 1971a) because the unique characters of the rostrum highlighted by that author for juveniles ≥8 mm CL persisted in our study for small juveniles (<8 mm CL). We also found interspecific differences in the growth patterns given by the RL-CL relationship (slopes) and in the RL/CL ratio (intercept differences). These results have important implications. Dall et al. (1990) mentioned that the shape and increase in size of different body structures in crustaceans depend on the species, age, sex, and the surrounding environment. Our comparison of the regression lines between RL and CL of the two shrimp species analyzed in the present study, coming from Yalahau and Río Lagartos lagoons, showed unambiguously that the growth pattern, or degree of change in RL in relation to CL, differed between the two species at all sizes of the specimens. Different intercepts, on the other hand, implied that although the growth patterns may be the same over the size range measured (regression lines are almost parallel), the relative body proportions of both species are different. These differences are likely due to different growth rates at some earlier size (Haddon and Willis, 1995). Both types of difference imply that the relative proportions of the body, or the body shape, are distinct for the species analyzed (Haddon and Willis, 1995). An analysis of the RL-CL relationship revealed that, at a given CL, the RL in *F. brasiliensis* grows 1.23–1.29 times faster than in *F. notialis*. On the other hand, the marked differences in the RL/CL ratio imply that this morphometric character is species-specific and, at a given CL, the pink spotted shrimp has a consistently longer rostrum than southern pink shrimp, with a value of 0.70 as a point of separation between species. These results are also qualitatively observed in the shape and position of the rostrum with respect to the segments and the flagellum of the antennule in both species.

In conclusion, we successfully separated small juveniles of two shrimp species that are found in coastal lagoons of the Gulf of Mexico. Both species can be identified by easily observed and quantified rostrum characteristics.

Acknowledgments

This work is part of the Ph.D. thesis of M. A. May-Kú at CINVESTAV-Mérida. Financial support from CONACyT México (grant to M.A. May-Kú) is acknowledged. The authors are grateful to M. Ornelas-Roa from the Plankton Laboratory at CINVESTAV-Mérida for her help in obtaining morphometric data. Two anonymous referees provided useful suggestions that significantly improved the manuscript.

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Exploring intraspecific life history patterns in sharks

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Marine ecosystems compose the major source (85%) of world fisheries production (Garcia and Newton, 1997). Although only a few fish species tend to dominate fishery catches (Jennings et al., 2001), a large diversity of fishes representing varied taxonomic levels, ecological guilds, and life histories is commonly taken. Recently, 66% of global marine resources were determined to be either fully, heavily, or over-exploited (Botsford et al., 1997). Considering the current state of many fisheries, the large diversity of species taken globally, and the general lack of resources to adequately assess many stocks, it has become important to develop shortcuts that may provide methods fisheries scientists can use to determine which stocks are in danger of overexploitation and which recovery plans are appropriate when biological data are limited (Stobutzki et al., 2001).

Applications of life history theory have proven a potentially useful means to accomplish such tasks (Stearns, 1992; Reynolds et al., 2001). Life history traits such as maximum size and age, maturity, mortality, and growth are correlated among teleost fishes (Adams, 1980; Winemiller and Rose, 1992; Gunderson, 1997; Cortés, 2000) and the relationships among such traits can be used to infer some general life history patterns. These general patterns reveal that teleost fishes with higher maximum ages tend to be larger, mature later, grow more slowly, and have lower natural mortality rates (K-selected species, Adams, 1980), whereas teleost fishes with lower maximum ages tend to show the opposite relationships (r-selected species, Adams, 1980). Correlations among traits may also allow one to approximate difficult to measure life history traits from traits that are easier to measure and possibly anticipate response to exploitation rates where life history data are limited (Jennings et al., 1999).

Applying these patterns to fisheries trends reveals some consistent and useful explanations. Jennings et al. (1998) found that teleost fishes from the northeast Atlantic that have decreased in abundance are generally K-selected species. Jennings et al. (1999) demonstrated that tropical teleost fishes of greatest maximum sizes were most vulnerable to exploitation. And Rochet (2000) illustrated the limitations of life history plasticity to compensate for heavy fishing pressure among four orders of teleosts.

Elasmobranchs, and particularly sharks, have also shown life history patterns similar to those of teleosts (Cortés, 2000; Frisk et al., 2001). Cortés (2000) offered three general life history patterns for sharks: 1) large litters, moderate to high longevity, large size, small offspring, slow growth, 2) small litters, high longevity, large size, large offspring, slow growth and 3) small litters, low longevity, small size, small offspring, fast growth. Simplified applications of the life history patterns have also been applied to elasmobranch fisheries. Smith et al. (1998) demonstrated that larger, later-to-mature Pacific shark species have lower rebound potentials (i.e., abilities to recover from fishing pressure), whereas Frisk et al. (2001) showed a similar pattern in sharks and rays in the north Atlantic. These relationships have been recommended as particularly useful when managing data-poor elasmobranch species (Musick et al., 2000).

As indicated by the above studies, variation in life history traits and patterns among shark species is well established (Cortés, 2000) and such relationships may be useful for the management of these fishes, but it is not known how these relationships may change within a species. Specifically, if and how do intraspecific life history traits of cosmopolitan species vary in different areas of the world? The spiny dogfish (*Squalus acanthias*) provides an alluring preamble to the topic: northeast Pacific spiny dogfish have been aged to 80+ years, and females mature at around 35 years (Jones and Geen, 1977; Saunders and McFarlane, 1993), whereas spiny dogfish in the north Atlantic obtain a maximum age of about 40 years, maturing at 12 years (Rago et al., 1998).

In the present study, I used generalized linear models (GLMs) to investigate whether spatial differences in life history traits, such as those seen in the spiny dogfish, reveal consistent patterns when compared with other spatially resolved life history information from other shark species. I then, as demonstration of potential utility, applied these models to predict life history trait values for areas lacking information for two species of shark, spiny dogfish (*S. acanthias*) and blue shark (*Prionace glauca*).

Materials and methods

Information for five life history traits (age at maturity, longevity (maximum age), mean fecundity, maximum size, and size at maturity) from 17 shark species in six families (Appendix, Table 1) for seven general areas (North Pacific (NP); North Atlantic (NoA); Gulf of Mexico (GM); Indian Ocean (I); Central Pacific (CP); South Pacific (SP); South Atlantic (SA)) was extracted from three primary literature sources (Smith et al., 1998; Cortés, 2000, 2002). Area distinctions were based on those by Cortés

Manuscript submitted 6 December 2004
to the Scientific Editor's Office.
Manuscript approved for publication
15 September 2005 by the Scientific Editor.
Fish. Bull. 104:311–320 (2006).

Table 1

List of shark species used in the analyses. Species abbreviations are used in tables and figures to simplify presentation.

Scientific name	Common name	Abbreviation
Carcharhinidae		
Carcharinus acronotus	Blacknose shark	Cac
Carcharinus amblyrhynchos	Grey reef shark	Cal
Carcharinus falciformis	Silky shark	Cfa
Carcharinus leucas	Bull shark	Cle
Carcharinus limbatus	Blacktip shark	Cli
Carcharinus longimanus	Oceanic whitetip shark	Clo
Carcharinus obscurus	Dusky shark	Cob
Carcharinus plumbeus	Sandbar shark	Cpl
Galeocerdo cuvier	Tiger shark	Gcu
Prionace glauca	Blue shark	Pgl
Rhizoprionodon taylori	Australian sharpnose shark	Rta
Sphyrnidae		
Sphyrna lewini	Scalloped hammerhead shark	Sle
Triakidae		
Galeorhinus galeus	Soupfin shark	Gga
Lamnidae		
Isurus oxyrinchus	Mako shark	Iox
Alophiidae		
Alopias superciliosus	Bigeye thresher shark	Asu
Squatinidae		
Squalus acanthias	Spiny dogfish	Sac
Squalus mitsukurii	Shortspine spurdog	Smi

(2000). Spatial resolution to the particular ocean basins in this study was defined by the information I was able to obtain, as were the choice of species and life history traits to analyze. Although other information for these and other species may be currently available, I limited my data to those found in primary peer-reviewed literature. When mean fecundity values were unavailable, the mean was assumed to be the middle value of the fecundity range given. Phylogenetic variance was controlled because I strictly evaluated intraspecific comparisons.

Initial data exploration was performed by visualizing intraspecific gender-based pairwise comparisons by area with dot plots (Fig. 1). Within each species and gender, the outcome of each comparison (i.e., the value for a particular trait in one area greater than, less than, or equal to that of another area) was evaluated. An overall relationship among areas for each life history trait was then constructed as a composite of each pairwise result. The purpose of this exercise was to visually explore the data and assess whether any intraspecific life history patterns by area were apparent.

A GLM framework was then used to construct simple models that quantitatively relate the effect of certain factors (e.g., area, gender, or taxonomic level) to a response variable—in this case to a particular life history trait. The flexibility of the GLM framework also allows one to consider non-normal response distributions while maintaining the advantages of linear regression (Venables and Ripley, 2002) by means of a link function relating the response variable mean to the linear predictors. I had no *a priori* knowledge of the variance structure for each life history trait (some of which will not have variance, given that they are maximum recorded values), so both lognormal (with an identity link) and gamma (with a log link) distributions were considered because of their appropriateness to continuous and nonzero data. Akaike's information criterion (AIC; Burnham and Anderson, 2002) was used to select among models, with the lowest AIC value indicative of the most appropriate model among all considered. Models explored included all combinations of the following factors: area, gender, and the taxonomic levels of species, genus, or family. Models that included the interaction between gender and area and gender and taxonomic level were also considered. Area effects and predictions of life history values among models with the use of the lognormal and gamma distributions were similar, but models with gamma error structure resulted in the lowest standard errors for area effects; thus a gamma error structure was ultimately chosen for each model.

Resultant model effects were used to compare area effects and to predict species- and gender-specific life history trait values for each area. The predicting models were then applied to two species (*S. acanth-*

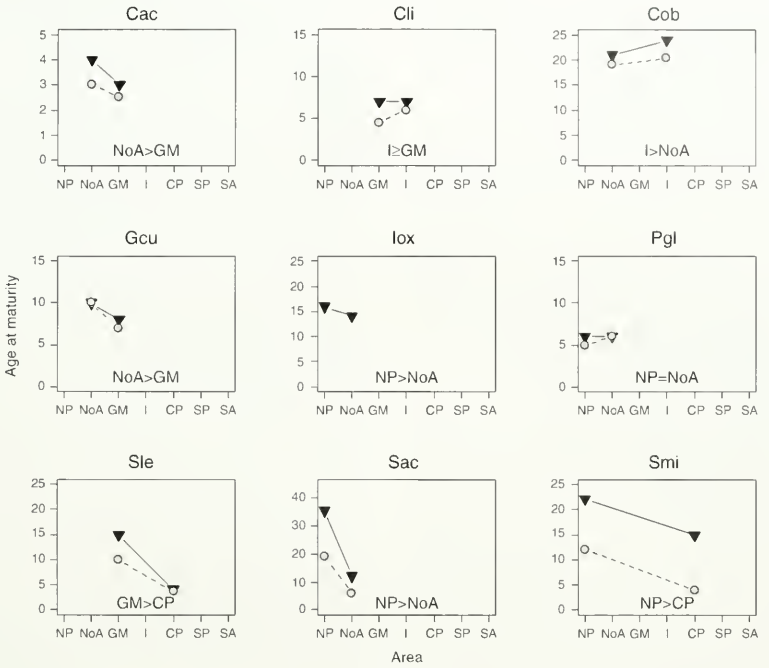

Figure 1

Example of plots used to evaluate the pairwise life history trait (*y*-axis) comparisons among areas (*x*-axis) by species (indicated by the abbreviation at the top of each panel). Gender-specific age at maturity (solid triangles=females; solid circles=males) is illustrated in this example, and the qualitative outcome of the pairwise comparisons is provided within each panel. A key to the species abbreviated names is found in Table 1. Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic.

ias and *P. glauca*) to demonstrate the calculation of life history trait values for areas with missing values. These species were chosen as examples because they are taxonomically different, are found in most of the area designations, and are represented by at least one pairwise comparison for each life history trait. Further investigation of the predictive capacity of these models to fecundity, size at maturity, and maximum size for the two species was performed by cross-validation: for each life history trait, *S. acanthias* or *P. glauca* data for one area were removed, the models were re-estimated, and predicted values for the newly missing area were calculated. Model fits to age at maturity, longevity, and male *P. glauca* size at maturity were not explored with cross validation because these data lacked the sufficient sample size needed to calculate the species effect once one area was removed (at least two remaining areas were needed).

Results

Model structure

For each life history trait that contained gender as a factor, the following final GLM model with a gamma distribution and a log link was selected (i.e., had the lowest AIC value):

$$\ln y_{A+sp\times g} = \ln \beta_A + \ln \beta_g + \ln \beta_{sp} + \ln \beta_{g\times sp}, \quad (1)$$

where β_A = area effect;
β_g = gender effect;
β_{sp} = species effect;
$\beta_{g\times sp}$ = gender and species interaction effect.
$y_{A+g\times sp}$ = value of the response variable (age, litter size, or length) for each area, species, and gender, accounting for the gender-species interaction.

This model is also biologically realistic because it includes the possibility that males in one species may be smaller than females and vice versa. For fecundity, the following model was chosen:

$$\ln y_{A+sp} = \ln \beta_A + \ln \beta_{sp}. \quad (2)$$

An assessment of Cook's statistic for all models revealed no evidence of any highly influential data points. A subsequent analysis of residuals by species indicated, in one case, a potential departure from the assumption that both genders of all species in all areas have the same variance. Highest residuals were reported for age at maturity in *S. acanthias*. Whether these high residual values are truly reflective of the species or an artifact of low sample size is unknown, so I carried forth with the analysis using the above models.

Area effects

Despite the low and unbalanced numbers of comparisons among coarse area designations, inter-regional variation and bias in sampling each life history trait, and the concomitant lack of power to resolve statistically significant relationships across all areas, a general and consistent trend emerged among the five life history traits. Intraspecifically, populations progressed from larger, longer-lived, later-to-mature populations in the northern-most latitudes to smaller, shorter-lived, and earlier-to-mature populations in the mid and southern latitudes (Fig. 2).

Predicting missing life history information by area

In addition to providing a comparison of the area effects on the response variables, the resultant predicting model offers a way to estimate missing life history values by area for each species and gender:

$$y = e^{(\beta_A + \beta_g + \beta_{sp} + \ln \beta_{sp \times g})}. \quad (3)$$

The factors β_g and $\beta_{sp \times g}$ in the above equation are not present in the fecundity predictions.

For both *S. acanthias* and *P. glauca* (Fig. 3), the predicted values mimicked the area trends of the reported values within two standard errors in all but one case (North Pacific *P. glauca* size at maturity was overestimated for both genders), and provided a means to estimate values for each life history by species and gender for areas not yet reported. The outlying cases may indicate an area (the North Pacific) where sampling is not representative of the true population (in this case, of *P. glauca*) and is in need of further investigation.

Cross validating models produced response variables similar to those of the full models in all but two cases (Fig. 4). In both cases (*S. acanthias* fecundity minus the South Atlantic, and *P. glauca* size at female maturity minus the North Pacific), the observed values were in opposite magnitude to that predicted. This difference could reflect either true relationships or possibly indicate areas that are undersampled (i.e., North Pacific for the size at maturity for female *P. glauca*).

Discussion

Knowledge of large-scale intraspecific spatial patterning in life history traits may be important when considering the population dynamics of a species, but such large-scale patterning has seldom been formally explored. Winemiller and Rose (1992) included median and range latitude correlations in their consideration of several life history variables of North American fishes, but comparisons were only interspecific. Vila-Gispert et al. (2002) demonstrated that fishes from higher latitudes north of the equator matured latest and had the highest fecundity, whereas fishes from South America had the lowest fecundity and earliest maturation, although these comparisons were again made interspecifically. Myers et al. (2001) described the relationship between maximum reproductive rate and carrying capacity among 21 stocks of Atlantic cod (*Gadus morhua*) in the North Atlantic using mixed effects models, but their analysis was done for only one species in a limited region. Helser and Lai (2004) also performed a similar analysis for individual growth rates in North American largemouth bass (*Micropterus salmoides*) populations and found latitudinal changes in growth rate.

Regarding elasmobranchs, Cortés (2000) considered trends in intraspecific reproductive traits for sharks but did not explicitly investigate the spatial patterning of those trends. Frisk et al. (2001) found regional differences across five areas for the spiny dogfish using three life history measures (maximum size, and size and age at maturity), but did not specify regional patterns. The authors also performed a similar analysis with several skate species, finding no difference among areas, but they considered only interspecific patterns. Cortés and Parsons (1996) compared the demography of two Floridian populations of the bonnethead shark (*Sphyrna tiburo*), which included several life history measures in the life table analyses, but the small spatial resolution was inadequate to indicate large-scale spatial life history correlations within this species. Lombardi-Carlson et al. (2003) extended the bonnethead shark investigation to a larger portion of the eastern Gulf of Mexico and found latitudinal variation in maturity and size, but again the scale of this study was relatively small. Additional small scale studies on intraspecific geographic variation in reproductive parameters of sharks have been presented by Horie and Tanaka (2002), Taniuchi et al. (1993), and Yamaguchi et al. (2000).

The results of the present study, specifically aimed at sharks as an example, indicate an emerging pattern for intraspecific life history variation, not unlike previously recognized interspecific patterns. Generally, there is a distinct difference in life history traits among areas—a pattern potentially useful when considering region-specific population dynamics. Across taxonomic designations, populations in the northern latitudes tended to be

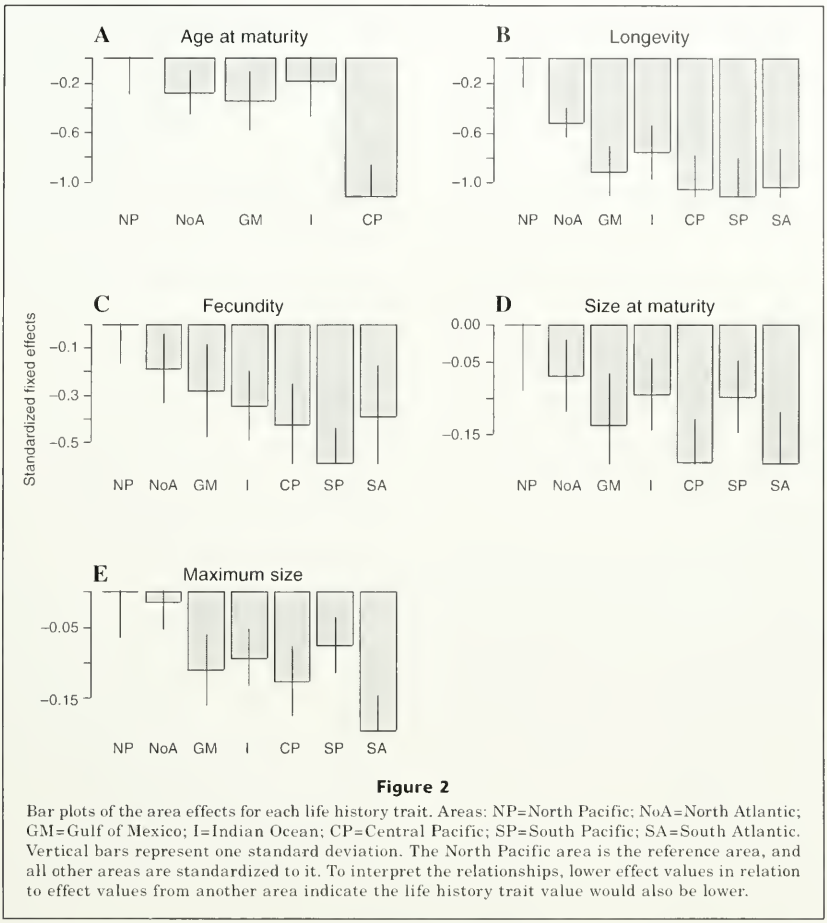

Figure 2

Bar plots of the area effects for each life history trait. Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic. Vertical bars represent one standard deviation. The North Pacific area is the reference area, and all other areas are standardized to it. To interpret the relationships, lower effect values in relation to effect values from another area indicate the life history trait value would also be lower.

larger, to mature later in life, to have longer life spans, and to have greater fecundity compared to conspecifics in the central and southern latitudes. Populations in the North Pacific, in particular, seem to demonstrate dramatic departures in life history measures compared to conspecifics in other areas. Therefore, instead of assuming life history information from one region should be applied to another region, the trends and predictive methods offered in the present study provide a means to extrapolate life history traits of cosmopolitan species in specific areas when only information from other areas is available; this method may prove useful for developing informative priors for Bayesian analyses (Punt and Hilborn, 1997). Caveats to these results include area-specific biases (i.e., certain-size individuals susceptible to capture) and errors in sampling programs and migratory patterns of specific species (e.g., individuals may be found in multiple areas during different parts of their life history). Thus a proper knowledge of the biology of the species is recommended before interpreting the interpolated life history values.

Other factors, such as fishing pressure, may influence regional differences in life history traits, challenging the interpretation of such patterns. Truncation of size and age classes, and reduction in age at maturity are recognized byproducts of heavy fishing (Longhurst, 1998a; Rochet, 2000). Although all the populations used in this study are and have been fished—some more intensely than others—this study assumes there is no consistent pattern to such exploitation in shark

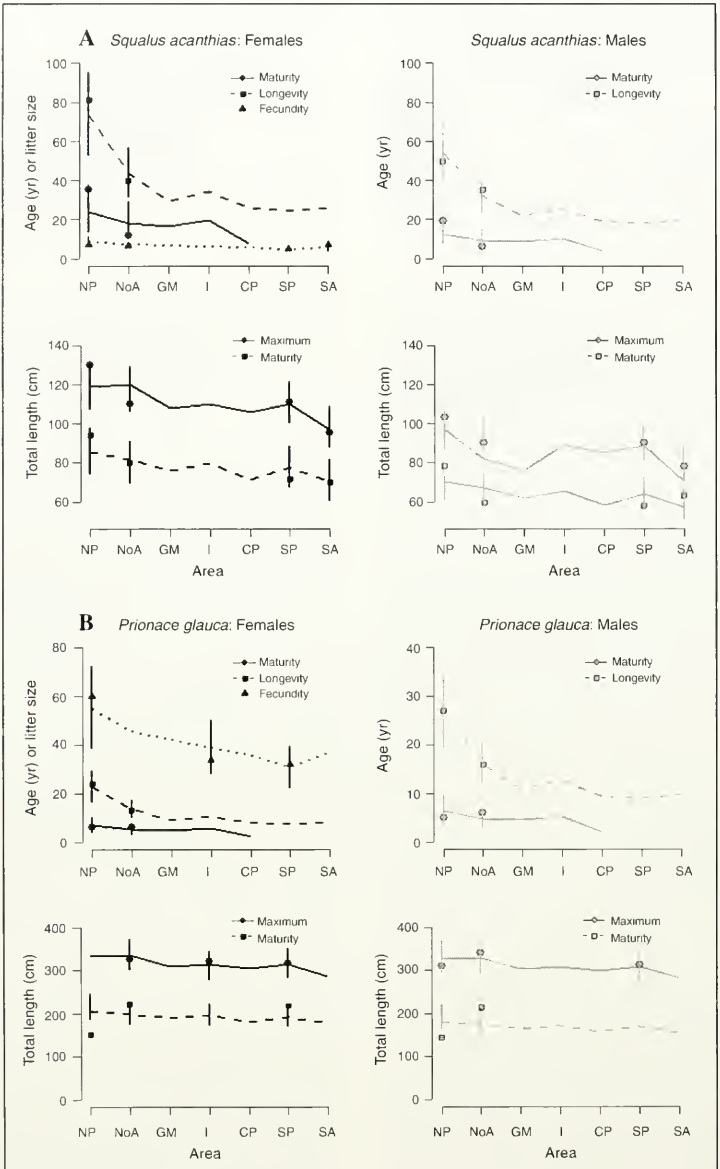

Figure 3

Example of predictive plots based on the results of the generalized linear models for each life history trait by gender for two species: (**A**) *Squalus acanthias* and (**B**) *Prionace glauca*. Lines represent predicted values and symbols represent values from the literature. Vertical lines represent two standard errors.

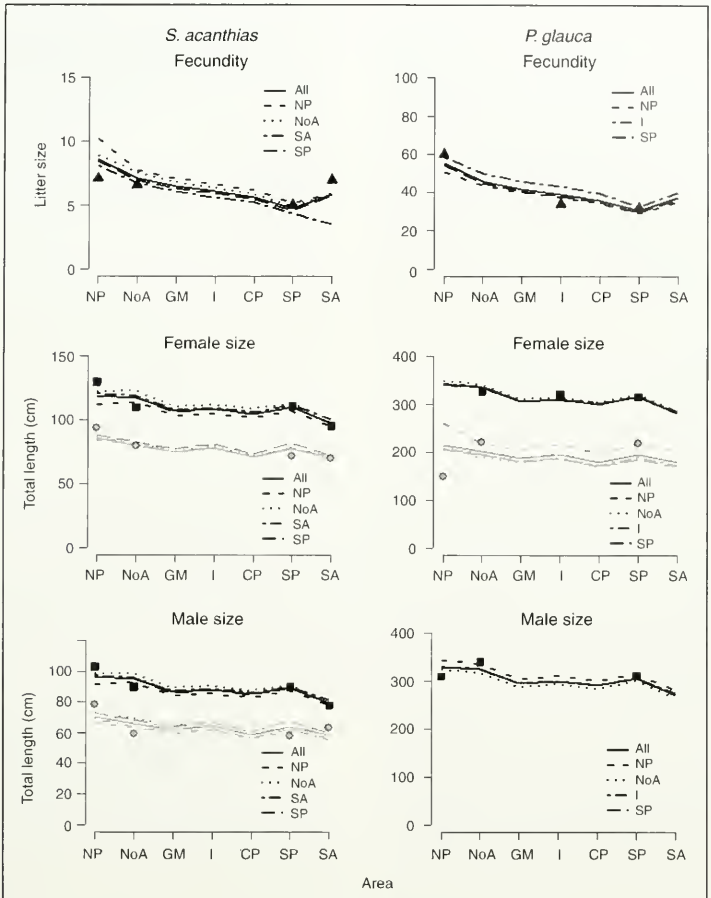

Figure 4

Plots of model predictions derived by cross validation for *S. acanthias* and *P. glauca*. Lines representing predicted value are distinguished as follows: "All"- all areas are included in the prediction; Lines denoted by area are predictions made without that area. Literature values are indicated as follows: triangles— fecundity, circles— size at maturity, squares—maximum size. Size at maturity for male *P. glauca* was not included because of insufficient data. Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic.

populations that would explain the results. Specifically, there is no reason to believe that species in the southern hemisphere have been more heavily fished than conspecifics in the northern hemisphere.

The results offered in the present study are based on small sample sizes in most areas, but hopefully they will bring attention to the usefulness of collecting spatially varying intraspecific information with the idea of constructing more robust models. Most investigations describing the patterns of shark life history traits suffer from insufficient biological resolution (either temporally or spatially) of the very parameters and subsequent relationships they attempt to explain (Smith et al., 1998; Cortés, 2000). Limited biological knowledge and

subsequent high uncertainty in the estimation of vital rates of many marine species, including elasmobranchs, is testimony to the fact that the accumulation of life history information should be a priority to biologists, fisheries scientists, and resource managers. Results from the models presented here could be used to hypothesize life history values in areas currently lacking information and thus be tested with further sampling in those areas. It is also hoped that the approach offered here may indicate areas where sampling may not be sufficient, as denoted by departures from the general model trend. Targeted sampling in that area would help resolve whether the departure is from a true area effect or species effect. As more data is gathered, it will be possible to explore other factors—such as temperature and guilds (e.g., coastal versus oceanic)—in the model structure.

Once steps are made to further resolve the species and area effects, one may start to ask questions regarding the cause of particular area effects. Potential mechanisms of true coarse-scale gradation of life history traits may be contained within the generalized characteristics of oceanic zoogeographic realms (Longhurst, 1998b), although a slightly less abstract mechanism could be found in the physical forcing events that characterize regions in the northern and southern hemisphere. Although both hemispheres demonstrate similar large-scale current and wind patterns, physical forcing events tend to be stronger in the northern hemisphere (Trenberth et al., 1998). Because this study offers coarse area designations to intraspecific life history variation, it is most likely a product of some macroscale characteristics of each region. Attention should therefore be directed towards large-scale characteristics of each region to explain these patterns, although small-scale dynamics are important for understanding each population's specific response to local environmental conditions (i.e., countergradient variation in growth rates [Conover, 1990; Conover and Present, 1990]).

It is becoming increasingly important to be able to assess fish stocks with minimal data. By combining genetic data revealing differing levels of intraspecific population substructure with the increasing number of studies demonstrating localized adaptations and plasticity in population parameters, it is apparent that intraspecific spatial differences must be considered in species management (Avise, 2000; Roff, 2002). Although the predictive power of this study may currently be weak because of low sample sizes, it offers a method to quantify potential spatial patterning in intraspecific life history traits that may allow responsible management of regionally data-poor species, and it may help frame future sampling protocols and studies of spatial patterns in life history traits.

Acknowledgments

I am grateful to André Punt, Joe Bizzarro, Gavin Fay, and Arni Magnusson for their many important comments regarding model structure and data use. I also thank Kristin Benshoof, Marilyn Cope, and three anonymous reviewers who contributed insightful comments that improved the presentation and clarity of this note.

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Appendix

Life history traits and area assignments for species used in the analyses. Sizes are total length (cm). Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic.

Species	Area	Maximum size		Size at maturity		Age at maturity		Mean fecundity	Longevity	
		F	M	F	M	F	M		F	M
Carcharinus acronotus	GM	130	122	110	103	3	2.5	5		
Carcharinus acronotus	NoA	154	164	120	110	4	3	5		
Carcharinus amblyrhynchos	CP	190	185	137	132.5			5		
Carcharinus amblyrhynchos	I	178	168	135	130			3		
Carcharinus falciformis	GM	308	314	235	217.5			11		
Carcharinus falciformis	NoA	330		234	218			10		
Carcharinus falciformis	I	283	244	248				11		
Carcharinus falciformis	SP	250	225	200	212.5			7		
Carcharinus leucas	GM	285		225	215			8		
Carcharinus leucas	I	300		239.5	239.5			9		
Carcharinus limbatus	GM	191	175	156	133	7	4.5	4.9	10	9
Carcharinus limbatus	NoA	202	189	156	143.5			4		
Carcharinus limbatus	I	247	246	208.5	201.5	7	6	6	11	10
Carcharinus longimanus	NoA	260		175				12.5		
Carcharinus longimanus	SA	250	235	185	185				17	14
Carcharinus longimanus	I	270	245	185	198					
Carcharinus longimanus	SP	270	251	200				6		
Carcharinus longimanus	CP	272	240	182	182			7	11	11
Carcharinus obscurus	NoA	371	360	284	279	21	19	11	39	39
Carcharinus obscurus	I	389	324	300	280	24	20.5	9.9	34	
Carcharinus plumbeus	CP	190	172	144	131			5.5		
Carcharinus plumbeus	NoA	234	226	183	180	15	15	9	32	40
Carcharinus plumbeus	I	199	190.5	169	167			8		
Galeocerdo cuvier	NoA	450		317.5	310	10	10	55	16	15
Galeocerdo cuvier	GM	450				8	7		11	9
Galeocerdo cuvier	I	410	370	340	290			35		
Galeocerdo cuvier	SP	428	350	287				31		
Prionace glauca	NP		310	150	145	6	5	60	24	27
Prionace glauca	NoA	327	340	221	215	6	6		13	16
Prionace glauca	SP	316	312	218				32		
Prionace glauca	I	321.5		214				34		
Rhizoprionodon taylori	SP	78	69	54	56			4.5		
Rhizoprionodon taylori	I	66	55	45	43			5		
Sphyrna lewini	GM	310	300	250	180	15	10		17	12
Sphyrna lewini	NP	324	305	210	198	4.1	3.8	26	14	11
Sphyrna lewini	I	346	301	200	150			16.5		
Galeorhinus galeus	NP	195	185	180	175					
Galeorhinus galeus	SP	174	175	140	135	15	17	28.4	53	41
Galeorhinus galeus	SA	155	148	128	117	17.5	13	23	36	36
Isurus oxyrinchus	NP	351		280		16			34	
Isurus oxyrinchus	SP	340	270	280	195			9		
Isurus oxyrinchus	NoA	375	298	280		14		13.5	23	9
Isurus oxyrinchus	I	333	271	266	199.5			11.5		
Alopias superciliosus	NoA	444	410	341	276			2		
Alopias superciliosus	NP	422	357	341	288	13	10	2	20	19
Squalus acanthias	NP	130	103	94	78.5	35.5	19	7.1	81	50
Squalus acanthias	NA	110	90	80	59.5	12.1	6	6.6	40	35
Squalus acanthias	SA	95.5	78	70	63			7		
Squalus acanthias	SP	111	90	71.5	58			5		
Squalus mitsukurii	NP	114	94	97.5	70	22	12	8.8		
Squalus mitsukurii	I	95	81	69	60			6.4		
Squalus mitsukurii	CP	91	82	69	48	15	4	3.6	27	18
Squalus mitsukurii	SP	104	102	85				3.5	16	14

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Volume 104
Number 3
July 2006

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Periodicals postage is paid at Seattle, WA. POSTMASTER: Send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn.: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

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U.S. Department of Commerce
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Volume 104
Number 3
July 2006

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Abstract—Standard and routine metabolic rates (SMRs and RMRs, respectively) of juvenile sandbar sharks (*Carcharhinus plumbeus*) were measured over a range of body sizes (n=34) and temperatures normally associated with western Atlantic coastal nursery areas. The mean SMR Q_{10} (increase in metabolic rate with temperature) was 2.9 ±0.2. Heart rate decreased with increasing body mass but increased with temperature at a Q_{10} of 1.8–2.2. Self-paired measures of SMR and RMR were obtained for 15 individuals. Routine metabolic rate averaged 1.8 ±0.1 times the SMR and was not correlated with body mass. Assuming the maximum metabolic rate of sandbar sharks is 1.8–2.75 times the SMR (as is observed in other elasmobranch species), sandbar sharks are using between 34% and 100% of their metabolic scope just to sustain their routine continuous activity. This limitation may help to explain their slow individual and population growth rates, as well as the slow recoveries from overfishing of many shark stocks worldwide.

Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change*

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Shark populations continue to suffer from overfishing throughout the Northwest Atlantic and worldwide (Baum et al., 2003). The sandbar shark (*Carcharhinus plumbeus*) can serve as a model for overfished coastal shark species, many of which share ecological and ecophysiological characteristics. After the rapid expansion of the Atlantic coastal commercial shark fishery in the mid-1980s, sandbar shark numbers declined 66% by 1991 (Musick et al., 1993; Sminkey and Musick, 1995). Like many of their K-selected relatives, sandbar sharks grow slowly and mature after a minimum of 13–15 years (Casey and Natanson, 1992; Sminkey and Musick, 1995). Demographic models of these species predict very slow rates of population increase even in the absence of fishing pressure, and elasticity analyses of these models demonstrate that the juvenile stage is the most critical life history stage (Sminkey and Musick, 1996; Cortes, 1999; Brewster-Geisz and Miller, 2000). It is necessary, therefore, to understand the actual and potential contributions of various juvenile nursery areas to recovery of the Northwest Atlantic sandbar shark population and to recovery of other coastal shark stocks (Branstetter, 1990).

Bioenergetics models can be used to assess the impacts and requirements of juvenile sharks as apex predators. Metabolic rate is the largest and most variable component of the energy budget for active fish species, and it is critical that it be determined accurately in order to construct realistic bioenergetics models (Ney, 1993). Systematic metabolic rate data for elasmobranchs are only rarely available, and previous models of sandbar shark bioenergetics have relied upon metabolic rate data from unrelated species (Medved et al., 1988; Stillwell and Kohler, 1993).

Manuscript submitted 21 August 2004 to the Scientific Editor's Office.
Manuscript approved for publication 26 September 2005 by the Scientific Editor.
Fish. Bull. 104:323–331 (2006).

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The lower Chesapeake Bay, Mid-Atlantic Bight, and adjacent coastal lagoon systems serve as the primary summer nurseries for sandbar sharks in the Northwest Atlantic (Musick et al., 1993). Juvenile sandbar sharks return for four to ten years to these nursery grounds, where they enjoy the benefits of generally high food availability and limited exposure to large shark predators (Musick and Colvocoresses, 1986; Grubbs et al., in press). Juvenile sandbar sharks in the nurseries are exposed to seasonal water temperature variations, as well as shorter time-scale fluctuations associated with their vertical movements and day to day variation. The minimum seasonal temperatures (≈15°C) occur in mid or late May, whereas the maximum temperatures (≈28°C) are reached in surface waters in July and August (Merson and Pratt, 2001). Throughout the day, sandbar sharks perform frequent vertical excursions and thus experience surface and bottom water temperatures that can differ by up to 5°C (Grubbs, 2001). Similarly, in Virginia's Eastern Shore lagoons, juvenile sandbar sharks venture onto broad, warm tidal flats at high tide and return to deeper, cooler channels as the tide recedes (Conrath[1]).

To improve bioenergetics models and to define critical habitat and the current suitability of nursery areas more accurately, standard (SMR) and routine metabolic rates (RMR) of juvenile sandbar sharks were measured over a relevant range of body masses (≈1 to 10 kg) and temperatures (18–28°C) (Merson and Pratt, 2001). This is the first direct measurement of SMR, and the first comparison of paired SMR and RMR, in a continuously active carcharhiniform species.

Materials and methods

All experiments were conducted at the Virginia Institute of Marine Science Eastern Shore Laboratory from June through September 2002. Sandbar sharks (57–124 cm total length; 1.025–10.355 kg) were captured by using hook and line from the surrounding tidal lagoon system and maintained in shoreside tanks (temperature 22–29°C, salinity 34–36‰). Individuals were fasted for at least 48 hours prior to use in an experiment to reduce any confounding effects of specific dynamic action (Medved, 1985).

Standard metabolic rates

Because sandbar sharks are continuously active obligate ram ventilators, SMR measurements were obtained from chemically immobilized and artificially ventilated animals maintained in flow-through, sealed box respirometers (Brill, 1979, 1987; Leonard et al., 1999). Respirometers were constructed of 0.85 cm thick acrylic, sized to accommodate the fish being studied, and covered with black plastic to minimize visual disturbance. Aerated and filtered seawater from a constant pressure head tank passed through the mouth and over the gills of the sharks, was mixed in the chamber by a small recirculating pump, and exited the respirometer by a hose mounted at the top. Water leaving the respirometer was collected, re-aerated, and mixed with a small amount of fresh filtered seawater to help maintain a constant temperature. Turnover rate for the system was 20–30%/hour (Steffensen, 1989).

Sharks were netted, injected with 0.4–1.8 mg/kg of the neuromuscular blocking agent pancuronium bromide through the caudal vein, and returned to the holding tank until they were unable to swim (typically 1–2 min). They were then placed supine on a moist towel and ventilated with aerated seawater while electrocardiogram (EKG) wire leads were inserted subcutaneously over the pectoral girdle to monitor heart rate. Individuals were also given an intramuscular injection (0.2–1.2 mg/kg) of steroid anesthetic Saffan® (alphaxalone and alphadolone; Pitman-Moore, Uxbridge, UK) (Oswald, 1978). Two 20-gauge hypodermic needles were inserted into the dorsal musculature and used to administer supplementary doses of pancuronium bromide and Saffan® whenever any slight tail movement was observed.

The partial pressure of oxygen (PO_2, mm Hg) in the seawater was measured with a polarographic oxygen electrode (Radiometer A/S, Copenhagen, Denmark) mounted in a water-jacketed cuvette (maintained at the experimental temperature) and connected to a digital oxygen meter (Cameron Instruments Company, Port Aransas, TX). All equipment was calibrated to manufacturer's specifications. Oxygen level in the inflow water was measured hourly, and outflow water was otherwise monitored continuously. Water temperature, PO_2, and heart rate were recorded every 10 seconds with a computerized data acquisition system (Daqbook 120 with a DBK52 thermocouple expansion card; Iotech, Inc., Cleveland, OH). The inflow ventilation volume (V_g, L/min) was adjusted to keep oxygen extraction between 10% and 20%. Measured PO_2 values were converted to oxygen content (mg O_2/L) following Richards (1965) and Dejours (1975). Standard metabolic rate (mg O_2/h) was calculated by using the Fick principle (Steffensen, 1989). Because the effects of pancuronium bromide were not reversible, at the end of each experiment individuals were euthanized with a massive overdose of sodium pentobarbital injected into the caudal vein. Sex was then determined and they were weighed to the nearest five grams and measured (precaudal and total lengths).

Standard metabolic rate data for each individual were plotted against time and averaged over all hours (range 1–7 hours) after the outflowing PO_2 stabilized. Standard metabolic rate measurements were obtained at 24 ±1°C on 33 of the 34 animals. In addition, 18 animals were exposed to acute temperature changes (to 18 ±1°C or 28 ±1°C, or to both). Temperature change rates averaged 4.5 ±0.6°C per hour and 6.4 ±1.1°C per hour for cooling and heating, respectively, although these were not statistically different (t =–1.46, df=36, P=0.15). Data

[1] Conrath, C. 2004. Personal commun. Virginia Institute of Marine Science. 1208 Greate Road, Gloucester Point, VA 23062.

collection was not resumed until at least one hour after the chamber had equilibrated to the new temperature (Steffensen, 1989). In order to minimize any systematic errors, the direction of temperature change was not always the same. To quantify the effects of acute temperature changes on SMR and heart rate, Q_{10} values were calculated over the temperature ranges 18–24°C, 24–28°C, and 18–28°C by following the methods of Schmidt-Nielsen (1997).

Routine metabolic rates

An annular respirometer (1250 L; diameter 167 cm) was used to measure RMR (Bushnell et al., 1989; Parsons, 1990; Carlson et al., 1999). A cage (diameter 61 cm) was placed in the center to force the sharks to swim around the perimeter of the tank. Water temperature was controlled during an experiment at 24–26°C by adjusting room temperature.

Sharks were transferred to the respirometer and allowed to recover for 30–90 minutes. The tank was sealed and data recording continued until oxygen content was reduced by 15% (≈two hours). The tank water was then re-oxygenated before the next measurement by pumping the seawater through a membrane oxygenator (Medtronics, Inc., Minneapolis, MN) (Steffensen et al., 1984). A complete RMR experiment consisted of one to five iterations of this process.

Oxygen concentration (mg O_2/L) was measured with a YSI 57 oxygen meter by using a YSI 5739 polarographic electrode oxygen-temperature probe (Yellow Spring Instruments, Yellow Spring, OH). Water temperature and oxygen content were recorded at 20-second intervals with a computerized data acquisition system (model PCA-14, Dianachart, Inc., Oak Ridge, NJ). Routine metabolic rates (mg O_2/h) were calculated from the rate of decline in dissolved oxygen (mg O_2/(L×min)) and the volume of the respirometer (Steffensen, 1989). Swimming speeds (in body lengths per second, BL/s) were determined every 15–30 minutes by averaging the time required for the shark to complete three to six laps. To account for the increased costs of swimming in a circular path, recorded RMRs were corrected to straight line estimates (RMR_{sl}) by following the method of Weihs (1981).

Statistical analysis

Routine and standard metabolic rate data at each temperature were fitted to the allometric equation $MR = a \times M^b$ by using nonlinear, iterative Gauss-Newton regression (Brill, 1979, 1987). This technique provides more accurate estimates of the parameters than log-transformed linear regression (Glass, 1969). The likelihood ratio test statistic was used to test for differences in the allometric exponents (b) among temperatures and between SMR and RMR at 24–26°C. Analysis of covariance (ANCOVA) of log-transformed metabolic rate (with log-transformed mass as covariate) was also used to test the equivalence of the exponents (b) in the untransformed allometric equations. Differences in SMR and heart rate among temperatures were evaluated by using ANCOVA. Analysis of covariance with mass as covariate was used to test for differences in mean SMR Q10's and heart rate Q10's among the three temperature ranges. The relationship between the RMR-to-SMR ratio and body mass was assessed with linear least squares regression. Statistical analyses were performed in Statistica 6.1 (StatSoft, Inc., Tulsa, OK) and SAS, version 8.0 (The SAS Institute, Inc., Cary, NC), with $P<0.05$ taken as the limit for significance. All values reported are means ± standard error of the mean.

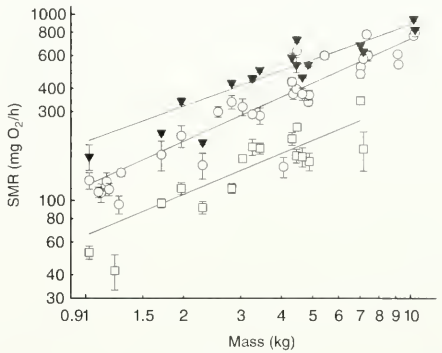

Figure 1

Standard metabolic rates (mg O_2/hr) of juvenile sandbar sharks (*Carcharhinus plumbeus*) as determined by flow-through box respirometry at 18°C (□), 24°C (○), and 28°C (▼). Lines show best-fit allometric equations at each temperature. Error bars indicate ±1 standard error.

Results

Standard metabolic rates

Standard metabolic rate increased with body mass (range 1.025–10.355 kg) at all three temperatures (ANCOVA, logmass, $F_{1,59}$=265.04, $P< 0.001$) (Fig. 1). The best-fitting allometric equations relating SMR (mg O_2/h) to body mass (M, kg) were

$$18°C: SMR = 65\ (\pm 15) \times M^{0.73\ (\pm 0.14)} \qquad n=16,\ r^2=0.71 \qquad (1)$$

$$24°C: SMR = 120\ (\pm 17) \times M^{0.79\ (\pm 0.08)} \qquad n=33,\ r^2=0.84 \qquad (2)$$

$$28°C: SMR = 207\ (\pm 28) \times M^{0.63\ (\pm 0.07)} \qquad n=16,\ r^2=0.87 \qquad (3)$$

Standard metabolic rate increased with temperature for each individual and overall (ANCOVA, temperature,

$F_{2,59}$=20.99, P<0.001). However, the allometric exponents (b) at each temperature were not significantly different (likelihood ratio test, χ^2_2=3.2, P=0.20; ANCOVA, logmass×temperature interaction, $F_{2,59}$=0.81, P=0.45).

The mean SMR Q_{10}'s were 3.2 ±0.4 for 18–24°C (n=14), 2.5 ±0.2 for 24–28°C (n=16), and 2.9 ±0.2 for 18–28°C (n=13). There was no overall effect of body mass on SMR Q_{10}'s (increases in metabolic rate with temperature) (ANCOVA, mass, $F_{1,36}$=0.04, P=0.84), but there was a significant negative correlation between mass and SMR Q_{10} for 24–28°C (P=0.014, r^2=0.36; slope=−0.20 ±0.07). The temperature range did not affect mean SMR Q_{10} (ANCOVA, range, $F_{2,36}$=1.37, P=0.27). The data sets were therefore pooled and the overall mean Q_{10} was 2.9 ±0.2 (n=43).

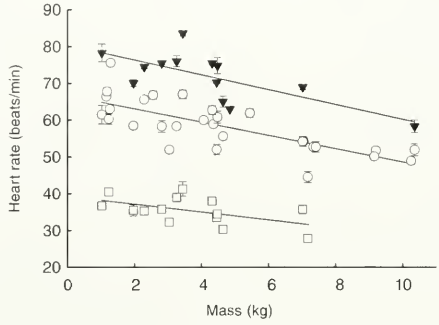

Figure 2

Heart rates (beats/min) of juvenile sandbar sharks (*Carcharhinus plumbeus*) (treated with pancuronium bromide) measured during standard metabolic rate experiments at 18°C (□), 24°C (○), and 28°C (▼). Solid lines represent best-fit linear regressions at each temperature as a function of body mass. Error bars indicate ±1 standard error.

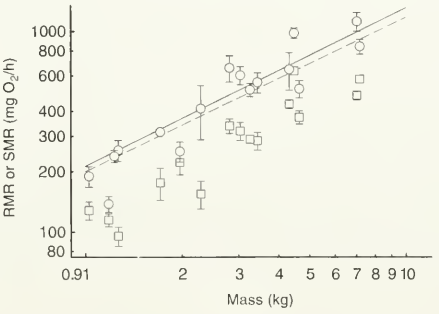

Figure 3

Paired routine (RMR, ○) and standard metabolic rates (SMR, □) (mg O_2/h) of 15 juvenile sandbar sharks (*Carcharhinus plumbeus*) at 24–26°C. Error bars indicate ±1 standard error. The solid line depicts the best-fitting allometric equation with the fish swimming in a curved path in an annular respirometer: RMR = 213 (±38) $M^{0.79(\pm 0.11)}$. The dashed line represents the best-fit allometric equation using the corrected straight-line swimming (RMR_{sl}) estimates: RMR_{sl} = 200 (±33) $M^{0.77(\pm 0.11)}$.

Heart rates

Heart rate was negatively correlated with body mass at all temperatures (ANCOVA, mass, $F_{1,50}$=29.99, P<0.001) (Fig. 2). The relationships between heart rate and body mass at each of the three temperatures were

$$18°C: \textit{Heart rate} = 39.3\ (\pm 2.0) - 1.07\ (\pm 0.49) \times M \qquad n=14,\ P=0.05,\ r^2=0.29 \qquad (4)$$

$$24°C: \textit{Heart rate} = 66.7\ (\pm 1.6) - 1.81\ (\pm 0.30) \times M \qquad n=29,\ P<0.001,\ r^2=0.58 \qquad (5)$$

$$28°C: \textit{Heart rate} = 80.4\ (\pm 2.9) - 2.02\ (\pm 0.61) \times M. \qquad n=13,\ P=0.01,\ r^2=0.50 \qquad (6)$$

Heart rate increased with temperature for each individual and overall (ANCOVA, temperature, $F_{2,50}$=64.21, P<0.001) (Fig. 2). However, the influence of body mass on heart rate did not vary among temperatures (ANCOVA, mass×temperature interaction, $F_{2,50}$=0.69, P=0.51).

The mean Q_{10}s for heart rate were 2.2 ±0.05 for 18–24°C (n=14), 1.8 ±0.04 for 24–28°C (n=12), and 2.1 ±0.03 for 18–28°C (n=11). Heart rate Q_{10} was not correlated with body mass (ANCOVA, mass, $F_{1,31}$=0.95, P=0.34). However, an overall significant effect of temperature range on heart rate Q_{10} was observed (ANCOVA, range, $F_{2,31}$= 4.68, P=0.02). 18–24°C and 18–28°C were significantly different from 24–28°C (P<0.001), but not from each other (P=0.08, Tukey unequal n HSD test).

Routine metabolic rates

Routine metabolic rate increased with increasing body mass (Fig. 3). The best-fitting allometric equation relating RMR (mg O_2/h) to mass (range 1.025–7.170 kg) was

$$RMR = 213\ (\pm 38) \times M^{0.79\ (\pm 0.11)}. \qquad n=16\ (53\ \text{trials}),\ r^2=0.82 \qquad (7)$$

The estimated additional costs of swimming in a curved path versus a straight line increased with body mass (range 0.8–19.9%; Fig. 3). With the straight-line swimming (RMR_{sl}) estimates, the allometric equation for RMR became:

$$RMR_{sl} = 200\ (\pm 33) \times M^{0.77\ (\pm 0.11)}. \qquad n=16,\ r^2=0.83 \qquad (8)$$

Although the acclimation periods in the annular respirometer were relatively short, it has been shown that

sandbar sharks recover rapidly from angling stress (6–10 h; Spargo et al.[2]). There was no evidence of systematic decreases in RMR (relating to recovery from handling stress) during individual RMR experiments, which averaged 16.2 ±2.0 hours in length. Using only the final trial for each individual, we fitted RMR to the allometric equation:

$$RMR = 203\ (\pm 35) \times M^{0.76\ (\pm 0.12)}. \quad n = 16,\ r^2 = 0.78 \qquad (9)$$

Routine (average ±SEM) swimming speeds decreased with increasing body size according to the exponential equation speed (bl/s)=3.54 $TL^{-0.43}$ (r^2=0.18) (Fig. 4). In most cases the animal maintained a swimming speed and direction along the outer wall of the chamber for 5–20 minutes before turning around. Because each shark swam at a relatively constant speed, the effect of swimming speed on metabolic rate could not be determined.

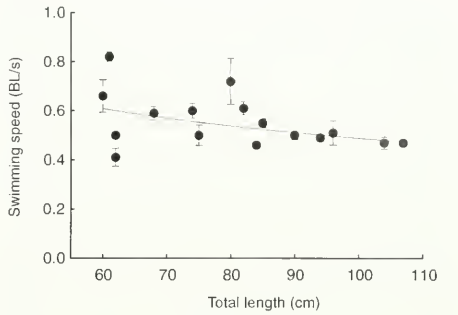

Figure 4

Mean (±1 SE) voluntary swimming speeds of sandbar sharks (*Carcharhinus plumbeus*) during RMR experiments. The solid line represents the best-fit equation: *speed* (*BL*/s) = 3.54×(*total length*)$^{-0.43}$.

Paired standard and routine metabolic rates

Paired SMR and RMR measurements were obtained for 15 sharks (1.025–7.170 kg) (Fig. 3). The mean ratio of RMR to SMR at 24°C was 1.8 ±0.1. The mean ratio of RMR_{sl} to SMR was 1.6 ±0.1. There was no significant correlation between body mass and the ratio of RMR to SMR (P=0.93, r^2<0.01). The allometric exponents for RMR and SMR at 24°C were also not significantly different (likelihood ratio test, χ^2_1=0.002, P=0.96; ANCOVA, logmass×type interaction, $F_{1,45}$=0.33, P=0.57).

Discussion

Effects of body mass and temperature on SMR and RMR

This study presents the first direct measures of SMR and expands the size range over which SMR and RMR have been reported for continuously active shark species (Fig. 5). Sandbar shark metabolic rate, like that of a wide variety of species, increases with increasing body mass according to the allometric equation $MR = aM^b$, with a b of ~0.71–0.79 (Schmidt-Nielsen, 1997). The effects of body mass on SMR, RMR, and RMR_{sl} (b in Eqs. 1–3 and 7–9) in sandbar sharks were similar to published values for other elasmobranchs (e.g., Pritchard et al., 1958; DuPreez et al., 1988; Sims, 1996). The temperature independence of b, previously reported for the lesser sandshark (*Rhinobatos annulatus*) and the bullray (*Myliobatus aquila*) (DuPreez et al., 1988), was evident overall in sandbar sharks. However, there was a significant effect of mass on SMR Q_{10} for the 24–28°C range. These two findings appear to contradict each other, but the 24–28°C pattern may be influenced by small sample sizes at larger body masses (only 2 sharks >7.5 kg).

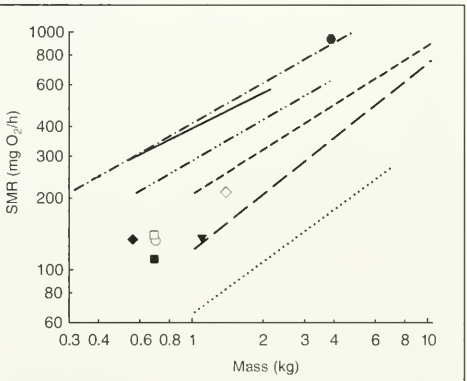

Figure 5

Standard metabolic rates of active elasmobranch species and tunas as a function of body mass: *Isurus oxyrinchus* 18°C (●, Graham et al., 1990); *Sphyrna lewini* 21°C (■), 26°C (○), and 29°C (□) (Lowe, 2001); *Negaprion brevirostris* 22–25°C (▼, Bushnell et al., 1989) and 25°C (◇, Scharold and Gruber, 1991); *Carcharhinus acronotus* 28°C (♦, Carlson et al., 1999); *C. plumbeus* 18°C (·····), 24°C (— — —), and 28°C (– – –) (present study); kawakawa (*Euthynnus affinis*) 25°C (———, Brill, 1987); yellowfin tuna (*Thunnus albacares*) 25°C (– · · –, Brill, 1987); skipjack tuna (*Katsuwonus pelamis*) 23.5–25.5°C (– · –, Brill, 1979). Lines are best-fit allometric equations at the stated experimental temperatures.

[2] Spargo, A. L., N. Kohler, G. Skomal, and R. Goodwin. 2001. The physiological effects of angling on post-release survivorship in juvenile sandbar sharks (*Carcharhinus plumbeus*). (Abstract.) American Elasmobranch Society 17th Annual Meeting, State College, PA. Website:http://www.flmnh.ufl.edu/fish/organizations/aes/abst2001d.htm [accessed on 26 September 2005.]

The effects of acute temperature change on SMR were consistent with published values for other elasmobranchs (Q_{10}≈2–3; e.g., DuPreez et al., 1988; Carlson and Parsons, 1999; Miklos et al., 2003). The Q_{10} for the SMR in elasmobranchs has also been reported to vary with the temperature ranges assessed (Butler and Taylor, 1975; Hopkins and Cech, 1994), but this was not the case for sandbar sharks. It is important to note the distinction between acute temperature changes and seasonal acclimatization when reporting Q_{10} values (Schmidt-Nielsen, 1997). In the present study, sandbar sharks were exposed to rapid temperature changes that mirrored short-term temperature fluctuations experienced in the wild (SMR Q_{10}=2.9 ±0.2). In seasonally acclimatized bonnethead sharks (*Sphyrna tiburo*), the effect of seasonal temperature change on metabolic rate was lower (Q_{10}=2.29–2.39; Carlson and Parsons, 1999).

Cost of activity and routine energy expenditure

The SMR is never realized in fish that must swim continuously to maintain hydrostatic equilibrium or to ventilate their gills. Measurement of SMR and RMR in active species nevertheless allows insight into the division of metabolic costs between swimming and maintenance processes. For example, the average metabolic rate of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in the wild was 1.4 times the estimated SMR (Lowe, 2002). In sandbar sharks, the RMR to SMR ratio (1.8 ±0.1) and RMR_{sl} to SMR ratio (1.6 ±0.1) were similar to those observed and estimated for several elasmobranch species (e.g., 1.5, Brett and Blackburn, 1978; 1.4, Nixon and Gruber, 1988; 1.7, Carlson et al., 1999). In other words, SMR comprises 56–63% of total metabolic rate at routine activity levels. Because the allometric exponents for RMR and SMR were not different at 24°C, we conclude that the RMR-to-SMR ratio (and, therefore, cost of activity) is also size independent, at least over the size range of sandbar sharks tested.

Our metabolic rate data span the size and temperature ranges relevant to the summer populations of juvenile sandbar sharks in Chesapeake Bay and other western Atlantic nursery areas (Grubbs et al., in press; Merson and Pratt, 2001). Bioenergetics models require estimates of field activity and corresponding energetic costs (Lowe, 2002). The swimming speeds of sandbar sharks in the annular respirometer (mean 0.55 ±0.03 bl/s) were well within the range of activity levels observed in nature (Grubbs, 2001). After the application of an oxycalorific coefficient of 13.6 J/(mg O_2) (Elliott and Davison, 1975), the RMR and RMR_{sl} for a 1-kg sandbar shark at 24°C represent energy expenditures of 69.7 and 63.4 kJ/day, respectively. These values are comparable to those for the lemon shark (*Negaprion brevirostris*, 67.7 kJ/day; Nixon and Gruber, 1988), *S. tiburo* (80.2 kJ/day; Parsons, 1990), and *S. lewini* (96 kJ/day at ~28°C; Lowe, 2002) . The Q_{10} values for SMR obtained between 18° and 28°C demonstrate that juvenile sandbar shark metabolic demands change significantly as ambient temperature changes, both on short time scales and over the course of the summer stay in the nursery areas.

Heart rates

Heart rate decreased with increasing body mass but increased with temperature (Fig. 2), as it does for other ectothermic species (Schmidt-Nielsen, 1997). Heart rates of juvenile sandbar sharks were comparable to heart rates of two other shark species while swimming (Scharold et al., 1989; Scharold and Gruber, 1991), although the sandbar shark data should be interpreted with caution. Pancuronium bromide has been shown to exhibit vagolytic activity in mammals (Melnikov et al., 1999), but to our knowledge its effect on shark heart rates is unknown and would depend on the resting vagal tone. In the dogfish (*Scyliorhinus canicula*), resting vagal tone increased with temperature between 7°C and 17°C (Taylor et al., 1977). The resting vagal tone and resulting elevation in heart rate after treatment with pancuronium bromide could be significant in sandbar sharks, especially at the higher temperatures. If so, Figure 2 may reflect the effect of temperature and body mass on intrinsic heart rate.

Measuring SMR of immobilized sharks

Standard metabolic rate is defined as the oxygen consumption of a postabsorptive-stage fish at rest, and it is considered the minimum metabolic cost of organismal maintenance (Brett and Groves, 1979). Two methods are commonly used to determine SMR. In the first, the slope of a power-performance curve relating the logarithm of oxygen consumption rate to relative swimming speed is extrapolated back to zero activity (e.g., Lowe, 2001). However, extrapolation does not take into account physiological differences between active and quiescent fish, specifically the induction of anaerobic metabolism during high-velocity swimming, and may misrepresent SMR (Brett and Groves, 1979; Cech, 1990). Further, swimming kinematics can be significantly altered in a swim flume, leading to overestimates of SMR (Lowe, 1996, 2001). The second option for measuring SMR is to confine the fish in a sealed or flow-through respirometer (e.g., Brill, 1987; Hopkins and Cech, 1994). This process works well for sedentary species, but active fish will struggle in such situations, requiring the use of paralytic and sedative agents, as well as artificial ventilation.

Several studies have confirmed, however, that the two methods yield identical results (SMRs and allometric exponents) in various fish species (e.g., yellowfin tuna [*Thunnus albacares*]; kawakawa [*Euthynnus affinis*]; skipjack tuna [*Katsuwonus pelamis*]; rainbow trout [*Onchorynchus mykiss*]; American shad [*Alosa sapidissima*]; aholehole [*Kuhlia sandvicensis*] [Brill, 1979, 1987; Dewar and Graham, 1994; Leonard et al., 1999]). Moreover, treatment with anaesthetics has been shown to have no effect on the SMR of little skate (*Raja erinacea*; Hove and Moss, 1997) or nursehound (*Scyliorhinus stellaris*; Baumgarten-Schumann and Piiper, 1968).

Because sandbar sharks are continuously active, we chose to measure SMR in immobilized and artificially ventilated animals in flow-through respirometers. As a check of this technique, a two-point power-performance curve was constructed by using the logarithms of self-paired SMR and RMR and the mean swimming speed of the animal in the annular respirometer. The average slope for 15 sharks (0.38 ±0.04) at 24–26°C was similar to the slopes of power-performance curves for four other ectothermic shark species (0.2, Scharold et al., 1989; 0.34, Scharold and Gruber, 1991; 0.38, Carlson et al., 1999; 0.32, Lowe, 2001), and we interpret these data as additional evidence that the technique provides acceptable results. This approach, moreover, avoids the expense and difficulties of developing a swimming tunnel large enough to accommodate juvenile sandbar sharks and may well be generally applicable for generating power performance curves in other continuously active fish species.

Elasmobranch metabolic rates and the cost of growth

The published SMRs of active elasmobranchs are well below those of high-energy demand teleosts (e.g., the endothermic tunas; Korsmeyer et al., 1996), with the exception of the endothermic mako shark (*Isurus oxyrinchus*) (Graham et al., 1990) (Fig. 5). Brill (1987, 1996) proposed that the high SMRs of tunas are an unavoidable consequence of their morphological, biochemical, and physiological adaptations for extremely high maximum aerobic metabolic rates, specifically that their large gill surface areas have led to high osmoregulatory costs (but see Brill et al., 2001). Most elasmobranchs, including the sandbar shark, have less than one third the gill surface area of a similar-size tuna (Muir and Hughes, 1969; Emery and Szcepanski, 1986). These modest mass-specific gill surface areas and corresponding low rates of oxygen delivery in ectothermic sharks likely dictate slow asymptotic growth rates (Pauly, 1981), in contrast to those of tunas, whose cardiovascular systems are adapted for meeting multiple metabolic demands (including growth) (Bushnell and Brill, 1991; Korsmeyer et al., 1996; Brill and Bushnell, 2001).

Significant levels of specific dynamic action (SDA, the elevation in metabolic rate in conjunction with protein synthesis after a meal [Brown and Cameron, 1991]) can probably not be met by the cardio-respiratory systems of elasmobranchs, particularly in continuously active species such as the sandbar shark, while they sustain routine activity levels. The oxygen consumption rate following a meal can exceed 2–3 times the SMR (DuPreez et al., 1988; Sims and Davies, 1994; Ferry-Graham and Gibb, 2001), whereas the RMR of sandbar sharks was 1.6–1.8 times SMR. Assuming that the maximum metabolic rate is 1.8 to 2.75 times the SMR (Scharold et al., 1989; Lowe, 2001), we determined that sandbar sharks are using between 34% and 100% of their metabolic scope just to sustain routine activity levels.

Given these limitations, sandbar sharks and other active elasmobranchs probably make tradeoffs among metabolic demands at the expense of SDA or growth to remain within their available metabolic scope, or they may adjust their behavior to seek cooler waters during digestion (Matern et al., 2000). Because rapid incorporation of ingested amino acids into body proteins is not possible, many elasmobranchs may have to reduce the rate of digestion or integrate SDA over a longer period (or do both). For example, estimated daily rations for several elasmobranch species average 1–2% of body weight per day (e.g., Bush and Holland, 2002; Dowd et al., 2006), compared to 4% or more in fast growing teleosts (e.g., Olson and Boggs, 1986). Not surprisingly, sandbar sharks in the Northwest Atlantic mature only after 13–15 years and grow less than 10 cm per year during that time (Sminkey and Musick, 1995). Growth rates for many other large, active elasmobranch species are also slow (Branstetter, 1990). Future research might well focus on exploring the relationship between SDA, active metabolic rates, and metabolic scopes of slow growing, continuously active sharks.

Acknowledgments

We thank Mark Luckenbach, Reade Bonniwell, and the entire staff of the VIMS Eastern Shore Laboratory for their hospitality, advice, and assistance in capturing and maintaining sandbar sharks. This work was supported through the National Shark Research Consortium (NOAA/NMFS grant no. NA17FL2813 to JAM); an Indiana University South Bend Faculty Research Award to PGB; and VIMS GSA Mini-Grant, William & Mary Minor Research Grant, and Oceanside Conservation Co., Inc., awards to WWD. We thank Medtronics for donating the membrane oxygenator used in the RMR experiments. All procedures were approved by the College of William and Mary Research on Animal Subjects Committee.

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Abstract—Using a bioenergetics model, we estimated daily ration and seasonal prey consumption rates for six age classes of juvenile sandbar sharks (*Carcharhinus plumbeus*) in the lower Chesapeake Bay summer nursery area. The model, incorporating habitat and species-specific data on growth rates, metabolic rate, diet composition, water temperature (range 16.8–27.9 °C), and population structure, predicted mean daily rations between 2.17 ±0.03 (age-0) and 1.30 ±0.02 (age-5) % body mass/day. These daily rations are higher than earlier predictions for sandbar sharks but are comparable to those for ecologically similar shark species. The total nursery population of sandbar sharks was predicted to consume ~124,000 kg of prey during their 4.5 month stay in the Chesapeake Bay nursery. The predicted consumption rates support the conclusion that juvenile sandbar sharks exert a lesser top-down effect on the Chesapeake Bay ecosystem than do teleost piscivores and humans.

Estimating consumption rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model*

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Manuscript submitted 29 October 2004 to the Scientific Editor's Office.
Manuscript approved for publication 15 September 2005 by the Scientific Editor.
Fish. Bull. 104:332–342 (2006).

The lower Chesapeake Bay, Mid-Atlantic Bight, and adjacent coastal lagoon systems serve as the primary summer nursery areas for the Northwest Atlantic Ocean sandbar shark (*Carcharhinus plumbeus*) population (Musick et al., 1993). Sandbar sharks are the most abundant large coastal sharks in the Mid-Atlantic Bight (Musick et al., 1993) and an important part of the commercial shark catch. After the rapid expansion of the fishery in the mid 1980s, the sandbar shark population in Virginia's coastal ocean waters declined by approximately 66% by 1991 (Musick et al., 1993). Meanwhile, catch rates in the lower Chesapeake Bay, the core nursery area for juvenile sandbar sharks, remained relatively stable (Musick et al., 1993). Because juvenile sandbar sharks return to the coastal or estuarine nursery grounds for the first four to six summers of life (Sminkey and Musick, 1995; Grubbs et al., in press), these nursery grounds are vital to the life history and potential recovery of the Northwest Atlantic sandbar shark stock (Branstetter, 1990; Hoff and Musick, 1990; Sminkey and Musick, 1996; Cortes, 1999).

Despite the abundance and position of elasmobranchs at the apex of many coastal and pelagic food webs, their energetic demands and the role of elasmobranchs as predators have rarely been quantified (Gruber, 1985; DuPreez et al., 1990; Sundström and Gruber, 1998; Lowe, 2002; Schindler et al., 2002). In the Chesapeake Bay, sandbar sharks occupy an apex position in the food web, preying upon

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Table 1

Parameters, distributions, and values used in error analyses of the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model. See text for parameter definitions. For parameters with triangular distributions, the initial estimates described in the text were assumed to be the most likely values.

Parameter	Distribution type	Mean or most likely value	SE or range	Source
SMRa	Normal	120.0	17.3	Dowd et al. (2006)
SMRb	Normal	0.788	0.076	Dowd et al. (2006)
Q_{10}	Normal	2.89	0.16	Dowd et al. (2006)
ACT	Normal	1.62	0.11	Dowd et al. (2006)
SDA	Triangular	0.10C	0.06–0.17C	DuPreez et al. (1988), Sims and Davies (1994), Duffy (1999), Ferry-Graham and Gibb (2001)
L_∞	Normal	164 cm	16.4[1]	Sminkey and Musick (1995)
t_0	Normal	–3.8 yr	0.38[1]	Sminkey and Musick (1995)
K	Normal	0.089	0.0089[1]	Sminkey and Musick (1995)
p	Normal	0.75	0.075[1]	Sminkey and Musick (1995)
F	Triangular	0.20C	0.17–0.38C	Wetherbee and Gruber (1993)
U	Triangular	0.07C	0.05–0.08C	Brett and Groves (1979), Duffy (1999)

[1] SE was assigned by the authors to yield a coefficient of variation of 10% (*sensu* Bartell et al., 1986)

a number of commercially important species such as menhaden (*Brevoortia tyrannus*), blue crabs (*Callinectes sapidus*), striped bass (*Morone saxatilis*), and bluefish (*Pomatomus saltatrix*) (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003). Interestingly, previous ecosystem models have predicted both significant (Stevens et al., 2000) and negligible (Kitchell et al., 2002) top-down effects of changes in shark biomass on ecosystem structure, depending primarily on the trophic complexity of the system and the incidence of omnivory (Bascompte et al., 2005).

Because the sandbar shark is one of the few species for which many of the necessary modeling parameters have been measured, it serves as an excellent system for assessing the bioenergetics and ecosystem role of large coastal elasmobranchs. This article has the following objectives:

1 to construct a realistic bioenergetics model for juvenile sandbar sharks in the Chesapeake Bay summer nursery grounds. Because previous sandbar shark models have suffered from a lack of species-specific data (Medved et al., 1988; Stillwell and Kohler, 1993), we have incorporated updated species-specific and habitat-specific data.
2 to use the model to assess the role of juvenile sandbar sharks as predators in the Chesapeake Bay to aid ecosystem modelers and fishery management efforts.
3 to test the sensitivity of the model to uncertainty in parameter estimates using error analysis to identify future research priorities (Kitchell et al., 1977).

Materials and methods

Study area and nursery habitat

The core sandbar shark nursery area (~500–1000 km^2; Grubbs and Musick, in press) in the lower, eastern Chesapeake Bay supports a seasonal population of ~10,000 individuals (Sminkey, 1994), composed almost entirely of sandbar sharks <90 cm precaudal length (PCL) (Musick et al., 1993; VIMS[1]). Juvenile sandbar sharks move actively throughout the nursery area, covering large activity spaces (>110 km^2) and the entire water column, as shown in telemetry studies (Medved and Marshall, 1983; Grubbs, 2001).

Sandbar sharks in the nursery area are exposed to both long-term and short-term changes in water temperatures. Juvenile sandbar sharks inhabit Chesapeake Bay at seasonal temperatures ranging from 15 to 29°C (VIMS[1]). During the months of July and August, a seasonal thermocline also develops in the lower Chesapeake Bay, which sandbar sharks will cross repeatedly throughout the day (Grubbs, 2001). The magnitude of the temperature gradient from top to bottom is typically 5–6°C (VIMS[1], Chesapeake Bay Program[2]).

[1] VIMS (Virginia Institute of Marine Science) Shark Ecology Program Longline Survey. 1973–2003. Unpubl. data (as a Microsoft Excel file). [Available from J. A. Musick. 1208 Greate Road, Gloucester Point, VA 23062-1346.]

[2] Chesapeake Bay Program Water Quality Database. Website: http://www.chesapeakebay.net/data/index.htm [accessed on March 2003.]

Bioenergetics model

Rates of anabolism, catabolism, and waste losses (Table 1) were used to construct a bioenergetics model that predicted daily energy consumption (C_D, in joules per day, J/d):

$$C_D = RMR_D + SDA + G_D + F + U. \quad (1)$$

The model used a daily time step, consistent with the determination of daily energy ration. Due to the reporting of the daily routine metabolic rate (RMR_D), specific dynamic action (SDA), fecal losses (F), and excretions (U) as fractions of consumption (see below), we rearranged Equation 1 and solved for C_D to yield the model:

$$C_D = \frac{RMR_D + G_D}{(1 - SDA - U - F)}. \quad (2)$$

We set the immigration and emigration dates for the simulation as May 15 and September 30, respectively (VIMS[1]).

We used the model to estimate daily energy ration for average individuals within each of six age-classes using the Chesapeake Bay nursery (Musick et al., 1993). In turn, we combined energetic requirements with diet composition data to estimate rates of food consumption (daily ration) and predatory impact of individual sharks over the course of the summer for each age class. Finally, these individual estimates were merged with estimates of population size and age structure to estimate the overall predatory demand of juvenile sandbar sharks in the Chesapeake Bay nursery area.

Model parameters

Routine metabolic rate (RMR) Like a number of carcharhiniform species, sandbar sharks are continuously active, which leads to high daily metabolic expenditures (e.g., Carlson et al., 1999). As a result, metabolic rate is the largest and most variable component of the energy budget for these active fish (Kerr, 1982; Boisclair and Leggett, 1989). Unfortunately, because of a paucity of available data, metabolic rate parameters are often borrowed from other species (e.g., Schindler et al., 2002). Sensitivity analyses have shown that accurate metabolic rate data are needed to construct realistic bioenergetics models (Kitchell et al., 1977; Bartell et al., 1986).

The allometric (size-dependent) influence on standard metabolic rate (SMR) in juvenile sandbar sharks was recently determined over the entire size range (42–92 cm PCL, 1–10 kg) characteristic of the Chesapeake Bay nursery area in flow-through respirometers for sharks treated with a neuromuscular blocker (Dowd et al., 2006). The best fitting allometric equation for SMR ($SMR = a \times M^b$) for 33 sharks at 24°C was

$$SMR_{24} = 120.0\ (\pm 17.3) M^{0.788\ (\pm 0.076)}, \quad (3)$$

where M = mass in kilograms; and
SMR = mgO_2 consumed per hour.

The values in parentheses are the standard errors of the allometric intercept and the allometric exponent estimates (hereafter $SMRa$ and $SMRb$, respectively).

Dowd et al. (2006) also determined the routine metabolic rate (the average oxygen consumption rate of a swimming shark) for 15 individual sandbar sharks at 24°C in an annular respirometer (diameter 1.67 m). The ratio of routine metabolic rate to SMR, corrected for the cost of swimming in a curved path in the respirometer (Weihs, 1981), averaged 1.62 ±0.11 (Dowd et al., 2006). This ratio was used in the model as a constant activity multiplier (ACT) to estimate field metabolic rate (*sensu* Winberg, 1960; Kitchell et al., 1977; Schindler et al., 2002). The ACT used is similar to those derived from field data for subadult *Negaprion brevirostris* (1.3; Sundström and Gruber, 1998) and juvenile *Sphyrna lewini* (1.45; Lowe, 2002). The sandbar shark ACT was assumed to remain constant for all age classes and over all temperatures (Dowd et al., 2006).

The effects of acute temperature changes (quantified as Q_{10}) on SMR for juvenile sandbar sharks (mass 1—10 kg) between 18° and 28°C have also been measured (Dowd et al., 2006). The overall mean Q_{10} (the relative increase in metabolic rate with temperature, scaled to a 10° temperature range) was 2.89 ±0.16 (n=43), was consistent over the size range of sharks tested, and was statistically indistinguishable among three treatments (18–24°C, 24–28°C, and 18–28°C). We assumed that the SMR Q_{10} remained constant throughout the simulation period.

For each day of the simulation, the Q_{10} was used to adjust the predicted SMR from Equation 3 to the simulated daily temperature (T) (equation adapted from Schmidt-Nielsen, 1997):

$$SMR_T = 10^{\left(\log SMR_{24} + \log Q_{10} \frac{(T-24)}{10}\right)}. \quad (4)$$

SMR_T was then multiplied by the ACT and by 24 hours to obtain the daily metabolic expenditure in mgO_2/day. Finally, this value was converted to daily metabolic energy utilization (RMR_D) by using the oxycalorific coefficient 13.59 J/mgO_2 (Elliott and Davison, 1975).

Specific dynamic action (SDA) Specific dynamic action represents the energetic cost of incorporation of digested amino acids into new proteins (Brown and Cameron, 1991). Although SDA varies with growth rate, or the protein content of ingested food (e.g., Ross et al., 1992), most bioenergetics models set SDA as a constant fraction of consumed energy (e.g., Hewett and Johnson, 1992). Fortunately, although SDA has been measured in only a few elasmobranch species, it is typically a relatively small fraction of consumed energy (DuPreez et al., 1988; Sims and Davies, 1994; Duffy, 1999; Ferry-Graham and Gibb, 2001). As an initial estimate, we assumed SDA to be 10% of consumed energy (Schindler et al., 2002).

Growth (*G*) Growth (G) is the change in energy stored in biomass and can be subdivided into somatic and reproductive growth outputs. We assumed the latter to be negligible because all the age classes in the sandbar shark bioenergetics model are at least 8 years from the age at maturity (Casey et al., 1985; Sminkey and Musick, 1995).

We employed a von Bertalanffy growth equation (Sminkey and Musick, 1995), based on a validated aging technique for sandbar sharks (Branstetter, 1987), to represent the precaudal length (PCL) of sharks of age y (y=0–5 **yr**) upon immigration (or birth) on May 15:

$$L_{yI} = L_{\infty}\left(1 - e^{-K(y-t_0)}\right) \quad (5)$$

where L_{∞} = 164 cm;
K = 0.089; and
t_0 = −3.8 years.

The PCL at emigration (L_{yE}) was determined by

$$L_{yE} = L_{yI} + p(L_{yI+1} - L_{yI}). \quad (6)$$

where p = the proportion of annual growth in PCL that occurs in the Chesapeake Bay nursery.

Analysis of vertebral rings indicates that annual growth of juvenile sandbar sharks occurs in two distinct phases: one period of rapid growth in the summer nurseries during which the sharks achieve roughly 75% of their annual growth in length, followed by a period of reduced somatic growth during the winter (Sminkey and Musick, 1995). Therefore, we assumed a p of 0.75 as an initial estimate. Limited tag-return data support this seasonal growth pattern. One juvenile (67 cm total length [TL] at tagging) was recaptured 0.5 km from the tagging location within the summer nursery in September 1998 by VIMS scientists; it had grown 3 cm TL after 44 days at liberty. Similarly, a juvenile sandbar shark of similar size that had been tagged and recaptured by NMFS scientists grew 3 cm in fork length (FL) (48–51 cm FL) over 62 days at liberty between mid-July and mid-September (Casey et al., 1985). In Delaware Bay, two sandbar sharks recaptured during the same summer grew 3 cm FL (45 cm flat tagging and 1 cm FL) (no size given) in 40 and 47 days at liberty, respectively (Merson and Pratt, 2001). In comparison, another juvenile (66 cm TL) was tagged in Chesapeake Bay in September 1995 and recaptured by VIMS scientists during the subsequent immigration period. This shark was at liberty for 225 days and grew only 3.5 cm TL during that time.

Both Medved et al. (1988) and Kohler et al. (1995) published equations relating mass to length for sandbar sharks. Because preliminary runs of the model demonstrated that these length-mass relationships yielded very similar results, we used the equation produced by Kohler et al. (1995) because it was derived from a larger number of individuals:

$$M = 0.0109\, FL^{3.0124}, \quad (7)$$

Fork length (FL) is in centimeters and mass (M) is in grams. Lengths were converted from PCL to FL and *vice versa* by using the regression (VIMS[1]):

$$FL = 1.0791\, PCL + 2.78. \quad (n=4385;\ r^2=0.99) \quad (8)$$

Specific growth rate (grams added per gram of body mass per day) was modeled by assuming that the mass of the shark increased by a constant proportion (x) in each of the n days of the simulation:

$$M_E - M_I = \sum_{D=1}^{n} x \times M_D. \quad (9)$$

M_D is the mass of the shark at the beginning of day D. No data exist to support an alternative pattern (e.g., growth varying with temperature or dissolved oxygen levels).

The mass of the shark on the first and last day (M_I and M_E, respectively) of the simulated nursery season was determined by using Equations 5–8. Fitted values for x in Equation 9 were on the order of 0.1–0.5% increases in mass per day. We used these values to calculate daily growth increments in grams per day and then multiplied by 5400 J/g of body mass (Cortes and Gruber, 1990; Lowe, 2002) to determine the daily increase in energy content.

Waste loss in feces (*F*) and excretions (*U*) A generally accepted value for total waste loss to excretions and fecal waste for carnivorous fishes and elasmobranchs is 27 ±3% of consumed energy (C) (Brett and Groves, 1979; e.g., Sundström and Gruber, 1998; Lowe, 2002; Schindler et al., 2002). This value was assumed for the sandbar shark in the present study, divided into F=0.20C and U=0.07C. Juvenile *N. brevirostris* have fecal waste losses between 38.1% and 16.9% (Wetherbee and Gruber, 1993), and excretory losses average 7% of ingested energy for a number of teleosts (Brett and Groves, 1979).

Water temperature data Surface and bottom water temperatures were obtained from the Chesapeake Bay Program's water quality database[2] for seven monitoring stations within the core sandbar shark nursery area in Chesapeake Bay for 1996–2002. Temperature measurements were averaged over all stations and over all years for each day of the simulation. The surface and bottom temperature readings were also averaged to obtain a mean water temperature for each day of the simulation in an average year. The simulated temperatures ranged from 16.8° to 27.9°C over the summer nursery season (mean 23.0° ±0.2°C).

Diet composition data Recent data detail the ontogenetic patterns of juvenile sandbar shark diet composition in and around Chesapeake Bay for sharks captured with longline and gillnet gears (Ellis, 2003). Diet data are represented by the index of relative importance. Index of relative importance combines the frequency, weight, and number of each prey type and is considered to have

Table 2

Diet composition data for juvenile sandbar sharks (*Carcharhinus plumbeus*) used to estimate daily rations and seasonal prey consumption. Prey species were grouped into four categories for each age class. Diet data, adapted from Ellis (2003), are expressed as index of relative importance. The average energetic content (J/g wet mass) of each prey type was calculated from data in Thayer et al. (1973).

Category	Representative species	Ages 0–1	Ages 2–3	Ages 4–5	Energy density (J/g)
Teleostei	Atlantic menhaden (*Brevoortia tyrannus*) Summer flounder (*Paralichthys dentatus*)	0.146	0.292	0.463	5050
Mollusca	Squids (*Loligo* spp.)	0.007	0.004	0.023	4390
Crustacea	Blue crab (*Callinectes sapidus*) Mantis shrimp (*Squilla empusa*)	0.847	0.672	0.421	4810
Elasmobranchii	primarily skates (*Raja* spp.)	—	0.031	0.094	5400

Table 3

Cohort sizes and estimated mean seasonal prey consumption in the lower Chesapeake Bay for each age class in the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model. Cohort sizes are mean ±SE.

Age class	Initial cohort size[1]	Indexed cohort size[2]	Seasonal prey consumption (kg)[3]				
			Teleostei	Mollusca	Crustacea	Elasmobranchii	Total
0	2545 ±216	4377 ±1074	4236	207	24,667	—	29,110
1	2122 ±284	2626 ±645	3634	178	21,157	—	24,969
2	2083 ±398	1837±451	6684	100	15,385	716	22,885
3	1698 ±417	1698 ±417	7757	115	17,855	831	26,558
4	900 ±184	900 ±184	7754	380	7053	1575	16,762
5	188 ±40	188 ±40	1900	93	1728	386	4,107
Total	9537 ±313	11,627 ±2483	31,965	1073	87,844	3,508	124,391

[1] Estimates are from Sminkey (1994).
[2] We retained the initial cohort size estimates for ages 3–5.
[3] Estimated by using mean indexed cohort size.

less bias than other diet indices (Cortes, 1997). For the present study, prey species were grouped into four categories for each age class of shark: teleost fishes, mollusks, crustaceans, and elasmobranchs (Table 2). The proportion of each prey type in the diet and the mean energy content values for each category (calculated from data in Thayer et al., 1973) were used to convert daily energy ration (kJ/d) to daily ration (percent body mass per day, %BM/d). Diet composition was assumed to remain constant during the simulation period. The average daily ration and total seasonal prey consumption were calculated for individuals of each age class.

Population estimates The relative abundance and size-class composition of the seasonal nursery population were estimated from catch per unit of effort (CPUE) data (Musick et al., 1993; VIMS[1]). Sminkey (1994) used virtual population analysis to estimate the sandbar shark cohort sizes in the Chesapeake Bay nursery from the VIMS Shark Longline Survey data, using the standard Mustad™ 9/0 J hooks between 1989 and 1993 (Table 3). However, the standard hooks select for larger animals, yielding underestimates of abundance for ages 0–2 years. Therefore, we indexed the VIMS CPUE data for ages 0–2, using smaller Mustad™ 12/0 circle hooks against the CPUE for larger hooks for 25 longline sets between 1997 and 2002 when both gears were fished simultaneously at the two lower Chesapeake Bay survey stations. We then used this index to produce a more realistic population age structure (Table 3). The mean adjusted nursery population size was 11,627 ±2483 individuals.

For simplicity, we assumed negligible mortality and zero emigration of juvenile sharks during the simulation period. Consequently, the revised cohort sizes were held constant throughout the simulation period. Low natural mortality rates would be expected for these sharks, particularly in light of the near absence of large coastal shark predators in the nursery (Musick et al., 1993). Tracking, tagging, and survey data all indicate that juvenile sandbar sharks remain within the nursery throughout the summer (Grubbs et al., in press; Merson and Pratt, 2001).

Model calculations

For each daily time step of the model and for each age class, RMR_D and G_D were calculated as described above. These estimates were used to solve for daily consumption in joules in Equation 2, where *SDA*, *U*, and *F* are the fractions of consumption described above. These daily energy consumption estimates were summed to determine total energy consumption for an average individual of each age class during the entire stay in the Chesapeake Bay nursery. Mean daily energy ration (DER) was calculated in kJ/d. The daily energy ration was also expressed as a percentage of the average total energy content (%DER) for each day:

$$\%DER = 100 \cdot \frac{C_D}{\left(\frac{M_D + M_{D+1}}{2} \cdot 5400\right)} . \quad (10)$$

Finally, gross conversion efficiency (K_1), the fraction of consumed energy that is devoted to growth, was calculated for each day:

$$K_{1_D} = \frac{G_D}{C_D} . \quad (11)$$

This value was used as a general test of the model outputs.

Error analysis

Static models were run by using the initial parameter estimates described above to determine point estimates of consumption. *SDA* and energy losses in *U* and *F* were modeled as constant fractions of consumption. The initial choices of these values, therefore, had a direct effect on the predicted consumption rates. Further, a number of the model parameters were measured with some uncertainty. A stochastic, Monte Carlo simulation routine (Crystal Ball© 2000 Academic Edition, vers. 5.2.2, Decisioneering, Inc., Denver, CO) was used to assess this uncertainty with error analysis (Bartell et al., 1986). Error analysis is particularly useful for evaluating model sensitivity to parameters that enter the model in a nonlinear fashion (Bartell et al., 1986), such as the SMR allometric exponent (SMRb) and allometric constant (SMRa) and the Q_{10}. The simulation randomly drew values from probability distributions for each model parameter (Table 1) for each of the 2000 Monte Carlo iterations. The model parameters were ranked in importance by their relative contribution to the variance of the stochastic model outputs (Bartell et al., 1986).

Results

Consumption rates

The model predicted mean daily energy rations (DER) increasing from 233 ±5 kJ/d (%DER=1.95 ±0.03%) for young-of-the-year to 784 ±16 kJ/d (%DER=1.20 ±0.02%) for an age-5 juvenile. These values correspond to prey consumption rates of 2.17 ±0.03%BM/d and 1.30 ±0.02%BM/d, respectively (Table 4). The predicted daily rations for a given age class over the course of the simulation period fluctuated with temperature because of the thermal influence on metabolic rate.

Table 4

Gross conversion efficiency (K_1), daily energy ration (DER), daily ration (DR), and total seasonal prey consumption (C_{tot}) for individuals of each age-class of the sandbar shark (*Carcharhinus plumbeus*) in the bioenergetics model. DER and DR were averaged over the 138 days of the simulation (mean ±SE).

Age class	K_1	DER (kJ/d)	DR (%BM/d)	C_{tot} (kg)
0	0.16	233 ±5	2.17 ±0.03	6.6
1	0.15	333 ±7	1.89 ±0.03	9.5
2	0.13	442 ±9	1.67 ±0.03	12.5
3	0.12	555 ±11	1.52 ±0.03	15.6
4	0.11	669 ±14	1.39 ±0.02	18.6
5	0.10	784 ±16	1.30 ±0.02	21.8

During the 4.5-month stay in the Chesapeake Bay nursery area, the static model predicted total energy consumption of 269% of the total energy content for an age-0 shark (~32,000 kJ), declining to 165% (~108,000 kJ) for age-5 sharks. When merged with diet composition data, the model predicted that an age-0 shark would consume 6.6 kg (300% average BM) of prey per summer, and an age-5 juvenile would consume 21.8 kg (180% average BM). Therefore, the total sandbar shark population would consume 124,400 kg of prey over the course of the summer in the Chesapeake Bay nursery area (Table 3).

The average K_1 declined quickly with age from 16.3 ±0.3% of consumed energy for age-0 sharks to 10.0 ±0.2% of consumed energy by age five. Because growth plus routine metabolism comprised a constant proportion of the total energy budget in the static model, the proportion of consumption devoted to metabolism increased with age. Metabolism for age-0 sandbar sharks accounted for roughly 46% of ingested energy, increasing to 53% of the energy budget for age-5 juveniles. When growth was set to zero, we calculated the maintenance rations to be 63–80% of the rations when growth was included.

Error analysis

The relative contributions of each of the input parameters to the variance of the model outputs exhibited similar patterns for all age classes (Fig. 1). The von Bertalanffy parameters predicting size at age (L_∞, K) had consistently high ranks for their contribution to model variance, as did those describing the allometric scaling of standard metabolic rate (*SMRa, SMRb*). *F* also contributed significantly to the variance of the model outputs for all age classes (Fig. 1). The contributions

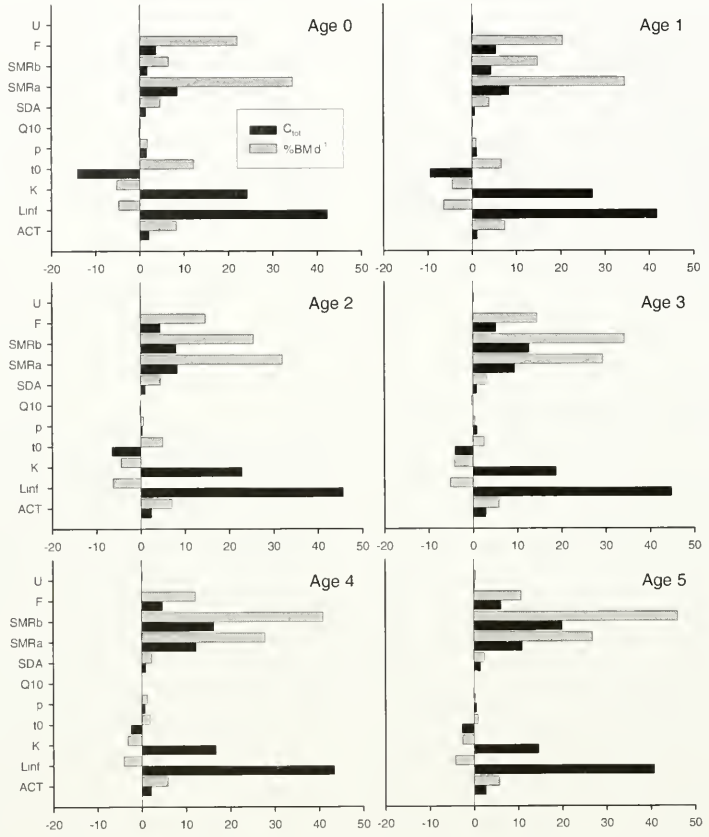

Figure 1

Results of the error analyses for the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model for ages 0–5 years, using the eleven parameters and distributions from Table 1 in 2000 Monte Carlo simulations. The horizontal axis is the percentage contribution of the variable of interest to the variance in two model predictions: total seasonal prey consumption in kg (C_{tot}, black bars) and mean daily ration (%BM/d, grey bars). Positive values indicate that an increase in the parameter yields an increase in the model output, and negative values indicate the opposite. See text for definitions of parameter abbreviations along the *y* axix.

of uncertainty in U, p, and Q_{10} were negligible for all age classes.

The Monte Carlo simulations predicted mean seasonal energy consumption rates 11–15% higher than those derived by using the static model. This elevation was primarily due to the fact that SDA and fecal waste (F) were allowed to comprise larger proportions of consumption than in the static model runs.

Discussion

Comparison with previous results

The mean daily rations for age-0 juvenile sandbar sharks predicted from our bioenergetics model (2.17 %BM/d, average M=2.2 kg) were higher than those previously reported (1.32 %BM/d, M=1.9 kg, Medved et al., 1988;

1.49%BM/d, M=1.7 kg, Stillwell and Kohler, 1993). This difference was partly due to the incorporation of species-specific routine metabolic rate data into our model, which were 8–15% higher than values from the spiny dogfish (*Squalus acanthias*) used in earlier models. Earlier models also estimated daily ration at a mean temperature over the entire year, whereas our model incorporated seasonal temperature shifts and the resulting effects on metabolic rate using the Q_{10}. Test runs of our model were used to predict daily rations over the winter, assuming that the diet composition was the same, 25% of annual growth occurred in the winter (Sminkey and Musick, 1995), and average water temperature was 14°C (Springer, 1960). These model runs predicted daily rations less than half (<1%BM/d) of those estimated for the summer nursery season. More data, however, are needed on the biology of sandbar sharks in the winter nursery grounds in order to develop an accurate year-round bioenergetics model.

Sandbar shark daily consumption rates have also been estimated by using meal size and frequency, as well as gastric evacuation rates. Our model's predicted consumption rates (1.30–2.17 %BM/d) support estimates based on meal size and frequency. The reconstructed meal size for juvenile sandbar sharks in Chincoteague Bay, based on stage of digestion estimates, was 4.23 ±0.31% BM (Medved et al., 1988). Given the sandbar shark's 70–92 hour gastric evacuation rate (Medved, 1985), as well as the high proportion of sharks landed with empty stomachs (17.9–20.0%) (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003), it seems likely that 48–72 hours pass between significant feeding events (Medved et al., 1985). Therefore, the reconstructed meal sizes correspond to daily consumption rates of 2.12–1.41% BM/d. In contrast, gastric evacuation models predicted juvenile sandbar shark daily rations (0.93% BM/d to 1.07% BMd; Medved et al., 1988) lower than our bioenergetics model. However, the data probably violated the gastric evacuation models' assumptions of continuous feeding and that time between meals exceeds digestion time (reviewed by Cortes, 1997).

The estimated sandbar shark daily rations are comparable to those for other active shark species. For example, the estimated daily rations for a 1-kg *N. brevirostris* and a 0.76-kg *S. lewini* were 2.62% BM/d and 2.9–3.9% BM/d, respectively (Gruber, 1985; Lowe, 2002). The sandbar shark daily rations were averaged over the entire simulated nursery season, during which temperature fluctuated by 10°C. Predicted daily rations in mid-summer were frequently higher than 3.0% BM/d.

The predicted mean gross conversion efficiency from our model (0.10–0.16) was similar to estimates for bull sharks (*Carcharhinus leucas*) fed to satiation in captivity (0.05–0.12, Schmid and Murru, 1994) and for juvenile lemon sharks (*N. brevirostris*) in the wild (0.10–0.13, Cortes and Gruber, 1994).

Parameter uncertainty

The largest potential sources of error in the model were L_∞, K, *SMRa*, and *SMRb* (Fig. 1). Fortunately, the von Bertalanffy growth parameters (L_∞, K) and the SMR allometric scaling parameters (*SMRa* and *SMRb*) are among the best known for juvenile sandbar sharks, and the initial estimates used are considered reliable. Metabolic rate may also be impacted by osmoregulatory costs incurred by penetrating the less saline regions (~20–25 ppt) of the Chesapeake Bay nursery area (Chan and Wong, 1977; Meloni et al., 2002). Future studies should investigate this possibility. Other confounding factors which will alter metabolic rate estimates associated with routine swimming behavior include movement of the animals with dominant tidal currents or burst swimming followed by oxygen debt repayments (or both factors) (e.g., Kerr, 1982; Boisclair and Leggett, 1989). Although these factors may affect ACT estimates, field tracking data from juvenile sandbar sharks indicate that mean rates of movement (converted to body lengths per second, BL/s) in the wild (0.23 BL/s, Huish and Benedict[3]; 0.46 BL/s, Medved and Marshall, 1983; 0.59 BL/s, Grubbs, 2001) are comparable with laboratory swimming speeds used to estimate the ACT (mean 0.55 BL/s; Dowd et al, 2006).

The effects of temperature on metabolism were not important in the error analyses, but two points merit consideration. Seasonal (e.g., winter vs. summer) metabolic rate Q_{10} may be lower than Q_{10} in response to acute temperature changes (Carlson and Parsons, 1999); future studies should address this possibility in sandbar sharks. The averaging of surface and bottom water temperatures in the model potentially obfuscated short-term changes in metabolic rate caused by sharks crossing the thermocline. Energetic implications of such short-term movements could be investigated with more detailed spatial models, but such an approach lies outside the scope of the present study.

Uncertainty in the fecal waste parameter accounted for a large portion of the variance in the stochastic model outputs, indicating that F should be investigated in sandbar sharks to refine the bioenergetics model. The effects of the slow gastric evacuation rate of the sandbar shark on the magnitude of the waste and SDA parameters are unknown.

One of the implicit assumptions of our model is that all energy spent is derived from food. Because juvenile sandbar sharks in the Chesapeake Bay nursery appear to grow steadily and rapidly (Sminkey and Musick, 1995), the assumption that the vast majority of energy is derived from food and not from energy reserves is probably justified. However, little is known about the feeding habits of sandbar sharks during their seasonal migrations or during their time in the winter nursery. At these times stored energy may play a greater role in the energy budget. Seasonal changes in energy content occur in Atlantic sharpnose sharks (*Rhizoprionodon*

[3] Huish and Benedict (1977) published their results under the species name for the dusky shark (*Carcharhinus obscurus*), but Grubbs (2001) noted that the size of the animals tracked was smaller than the size at birth for *C. obscurus*. Misidentification of the congeneric sandbar and dusky sharks is common.

terraenovae) (Hoffmayer, 2003); if such changes occur in sandbar sharks, these fluctuations could also affect the model's consumption estimates.

Ecosystem interactions

Our results downplay the top-down role of sandbar sharks in the trophic economy of the lower Chesapeake Bay. The model results presented above predict that juvenile sandbar sharks consume ~120,000 kg of prey in an average summer in the nursery. In comparison, the estimated annual prey consumption rates of the dominant teleost piscivores (bluefish, *P. saltatrix*; striped bass, *M. saxatilis*; and weakfish, *Cynoscion regalis*) in Chesapeake Bay were 27,000,000 kg, 10,000,000 kg, and 5,000,000 kg, respectively (Hartman and Brandt, 1995a). Moreover, the seasonal consumption of prey species by juvenile sandbar sharks is insignificant compared to fisheries landings. The total predicted consumption of Crustacea and Teleostei by juvenile sandbar sharks equals only 0.57% and 0.01% of the annual commercial landings of blue crabs (*C. sapidus*) and Atlantic menhaden (*B. tyrannus*) in Virginia, respectively (U.S. Department of Commerce[4]).

Bottom-up effects on sharks as apex predators are possible if lower trophic levels are overfished, but the apparent opportunistic foraging strategy of sandbar sharks (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003) probably reduces their vulnerability to declines of specific prey species (Stevens et al., 2000). However, if current fishery landings in Chesapeake Bay are not sustainable, the dietary overlap between the dominant piscivorous teleost species (Hartman and Brandt, 1995b) and sandbar sharks could lead to competition among these predators for limited prey.

Conclusions

An updated sandbar shark bioenergetics model predicts higher consumption rates than earlier bioenergetics estimates, but the daily ration estimates generally agree with reconstructed meal sizes from stomach contents data. Our results will be useful for ongoing efforts to build ecosystem-wide trophic models for the lower Chesapeake Bay.

As the sandbar shark population slowly recovers from overfishing, the contributions of the summer nursery grounds of the lower Chesapeake Bay to juvenile growth and survival will remain critical. Meanwhile, the slow growth rate and low consumption rate of these long-lived elasmobranchs in a complex trophic system may indicate a limited top-down ecosystem role for sandbar sharks in Chesapeake Bay. Our results support the conclusion that the effects of anthropogenic activities—fisheries and other activities—on shark populations often greatly outweigh the effects of these populations on their ecosystems (Stevens et al., 2000; Bush and Holland, 2002; Kitchell et al., 2002; Baum et al., 2003; Bascompte et al., 2005).

[4] United States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. Commercial Fishery Landings Database. Website: http://www.st.nmfs.gov/st1/commercial/index.html [accessed May 2004.]

Acknowledgments

This work was supported by the U.S. National Shark Research Consortium (NOAA/NMFS Grant no. NA17FL2813 to J.A.M.) and an Indiana University South Bend Faculty Research Award to P.G.B.

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Depredation of catch by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) troll fishery

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Abstract—We documented depredation by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) troll fishery. Between March and June 2003, we conducted 26 interviews of charter and commercial fishermen in Islamorada, Florida, and 23 along Florida's east coast from Fort Pierce south to Lake Worth Inlet. All fishermen indicated they had observed bottlenose dolphins depredating bait or catch—king mackerel being the species most often taken by dolphins. During on-board observations of depredation between March and June 2003, we found that dolphins took 6% of king mackerel caught by charter fishermen and 20% of fish caught by commercial fishermen. We concluded that depredation by bottlenose dolphin occurs commonly in this fishery and has the potential to incur a significant economic cost to king mackerel fishermen. To address this concern, we conducted preliminary tests of a gear modification designed to reduce depredation in the king mackerel fishery between December 2003 and January 2004. These tests demonstrated that a modification to the outrigger planer will successfully deter bottlenose dolphins from engaging in depredation, without causing a reduction in catch.

Manuscript submitted 16 September 2004 to the Scientific Editor's Office.

Manuscript approved for publication 16 September 2006 by the Scientific Editor.

Fish. Bull. 104:343–349 (2006).

Depredation is the removal of or damage to captured fish or bait caused by marine predators. Evidence of depredation exists for several pinniped and cetacean species (Yano and Dahlheim, 1995; Reeves et al.[1]; NRC, 2003). A recent increase in the number of reports of depredation by marine mammals may reflect changes in fishing effort, increased spatial overlap between these predators and fisheries, or behavioral learning among marine mammals (Donoghue et al.[2]). With a rapidly growing human population, fishing effort in coastal regions will likely continue to increase, causing even greater conflicts between fisheries and marine mammal populations throughout the world's oceans (Read, 2005).

Marine mammals engaging in depredation cause damage to fishing gear, decrease the value and quantity of catches, and reduce catch by dispersing fish (Reeves et al.[1]). Depredation may benefit marine mammals by increasing foraging success, but the behavior, habitat, and distribution of mammals may change as they frequent areas of high fishing effort (Reeves et al.[1]). Harmful consequences of depredation to marine mammals may include injury or mortality from entanglement with fishing gear or from the retaliatory measures of angry fishermen.

Our purpose in this study was to document the extent, nature, and cost of depredation by bottlenose dolphins (*Tursiops truncatus*) in the king mackerel (*Scomberomorus cavalla*) charter and commercial fisheries of Florida. There have been previous anecdotal reports of depredation by dolphins in this fishery (Odell, 1975), but no systematic study of these interactions has been conducted. We also worked with fishermen to identify potential tools that would deter dolphins from engaging in depredation. Other studies have employed this approach with considerable success. For example, Noke and Odell (2002) modified the design of crab pots, and thus prevented dolphins

[1] Reeves, R. R., A. J. Read, and G. Notarbartolo di Sciara (eds.). 2001. Report of the workshop on interactions between dolphins and fisheries in the Mediterranean: evaluation of mitigation alternatives, 44 p. Istituto Centrale per la Ricerca Applicata al Mare, Rome, Italy. Website: http://www.cetaceanbycatch.org/Papers/Reeves.pdf [acessed on 12 March 2004].

[2] Donoghue, M., R. R. Reeves, and G. Stone. 2003. Report on the workshop on interactions between cetaceans and longline fisheries held in Apia, Samoa, November 2002. New England Aquarium Aquatic Forum Series Report 03-1, 44 p. Website: http://neaq2.securesites.net/scilearn/conservation/LonglineReport2002.pdf [accessed on 17 January 2004].

from opening pot doors and taking bait fish. Melvin et al. (1999) demonstrated a reduction in seabird depredation of salmon gill nets by combining the use of acoustic devices and mesh panels strategically placed in the upper portion of the gillnet as a deterrent to seabirds.

King mackerel are distributed along the east coast of the United States from Massachusetts to the Gulf of Mexico and Caribbean Sea (Gold et al., 2002). Two stocks of king mackerel occur in Florida, one that migrates along the Atlantic coast and the other that is found in the Gulf of Mexico (Schaefer and Fable, 1994; Gold et al., 2002).

King mackerel are captured primarily by trolling, in which a fishing vessel trails several fishing lines—either from fishing poles (on charter vessels) or from reels (on commercial boats). Both charter and commercial vessels use outriggers that help to prevent entanglement of multiple lines. Trolling is generally considered to be a "clean" fishery with little bycatch. By varying the size of hooks, lures, and choice of bait, fishermen effectively target particular species and limit the bycatch of undesired species (Alverson et al., 1994). Nontarget species are generally released and have a high probability of survival.

Commercial fishing operations in the United States yielded over 4.8 million pounds of king and cero mackerel (*Scomberomorus regalis*) during 2001. This commercial fishery was valued at almost seven million dollars, more than half of which was landed in Florida (O'Bannon, 2002). During 2001–02, commercial fishermen captured more than two million tons of Atlantic king mackerel, sixty percent of which was caught in Florida, whereas recreational fishermen reported catching about four million tons of fish from the same stock, and about fifty-eight percent of this catch was taken in Florida (NMFS[3]).

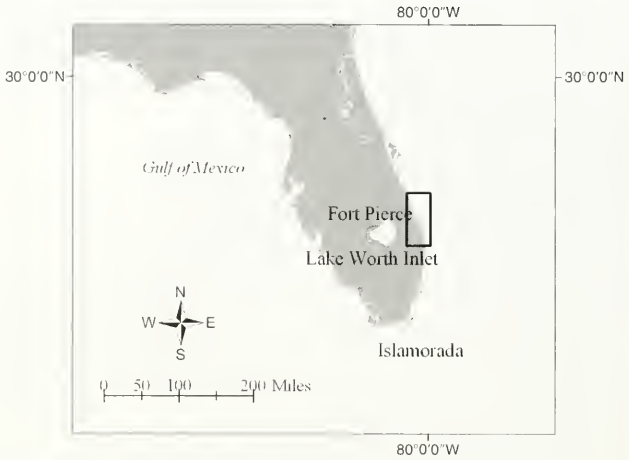

Figure 1

Survey area for bottlenose dolphin (*Tursiops truncatus*) depredation on the king mackerel (*Scomberomorus cavalla*) fishery in Florida. (Source of map: Florida Fish and Wildlife Conservation Commission; adapted by present authors.)

Materials and methods

Study sites

We selected two coastal regions of Florida: 1) Islamorada in the Florida Keys and 2) along the eastern coast, from Fort Pierce south to Lake Worth Inlet, for our study (Fig. 1). These regions represent areas in which commercial and charter fisheries for king mackerel exist during at least part of the year. Islamorada draws thousands of tourists each year to its charter fleet; the east coast of Florida boasts a thriving commercial king mackerel fishery.

Interviews with fishermen

From March through June 2003, we interviewed fishermen, using the face-to-face method of Rea and Parker (1997). We selected captains of offshore fishing charter boats or commercial king mackerel fishermen in the study sites to participate in this study. Because of the multi-use nature of fishing vessels, we included commercial, charter, and recreational vessels as options of vessel type on the survey.

Observations of dolphins

We conducted observations from the flying bridge of the charter boats and from the stern of the commercial vessels from March to June 2003. We recorded positional coordinates every 30 minutes with a hand-held GPS unit. During each 30-minute interval, we recorded vessel activity (transit to and from fishing grounds, or active fishing) and further categorized the fishing activity, depending on the target species.

For each 30-minute period, we recorded the behavior and estimated the number of dolphins sighted during the interval. We defined the following behavioral categories:

Depredation	a dolphin was observed consuming bait or captured fish from the lines
Begging	a dolphin approached a vessel in order to obtain food

[3] NMFS (National Marine Fisheries Service). 2003. Stock assessment analyses on spanish and king mackerel stocks, 147 p. Prepared for the 2003 mackerel stock assessment panel meeting. Sustainable Fisheries Division Contribution SFD/2003-0008, NMFS, Southeast Fisheries Science Center, Sustainable Fisheries Division, 75 Virginia Beach Drive, Miami, FL 33149.

Eating discarded bait	a dolphin consumed bait thrown from a fishing vessel
Milling near the boat but not interacting with the boat	a dolphin was in the same area as the fishing vessel but did not seek food or become entangled in gear.
Following the boat	a dolphin was actively following or pursuing the boat
Passing the boat or being passed by the boat	a dolphin was observed traveling or was passed by the vessel, but the dolphin neither followed nor interacted with the vessel

Impact on the king mackerel fishery

To assess the extent and impact of depredation on the king mackerel fishery, we recorded the type of fishing gear, the number and species of fish caught, and the number and species of fish lost or damaged by depredation during each 30-minute fishing interval. We attributed lost fish to bottlenose dolphin depredation if we observed dolphins following the boat or chasing the fish. We recorded the species of the fish if a definitive part of the fish was retrieved or if we observed the fish before depredation occurred. We also recorded the fishermen's response to depredation. The categories of response included leaving fishing grounds, ignoring dolphin depredation, throwing objects or shooting, cutting fishing line, or increasing boat speed.

Testing a deterrence device

We also worked with fishermen to devise and test a deterrence device to be used on outriggers of commercial fishing vessels. The device was equipped with a planer that is used on outrigger lines. An outrigger release clip was secured to the back of the planer (Fig. 2). The bait line passed through the outrigger clip, which released when a fish bit on the bait. The clip also released a metal wire that was attached to the bait line. The wire traveled towards the fish and flapped around the fish at the end of the bait line, making it difficult for a dolphin to approach the fish.

We tested the device on commercial fishing vessels in Fort Pierce during December 2003 and January 2004. We randomly placed the device on one of two outriggers, noting on which of the two outriggers the device was placed and the time and GPS coordinates for each event. An event occurred when the fishing line was placed in or taken out of the water and when a fish was caught or depredated. We recorded the number and species of each fish that was caught, taken, or damaged.

Results

Interviews with fishermen

We conducted interviews with 26 king mackerel boat operators in Islamorada and 23 operators along Florida's east coast. Several individuals indicated that their boats served multiple purposes or that they operated different types of boats during different times of the year (Table 1).

All fishermen responded that they saw or interacted with bottlenose dolphins while fishing. Forty-seven fishermen provided useful responses to questions regarding depredation; all of these respondents indicated they had observed dolphins taking bait or catch. Other reported interactions included entanglement in fishing gear (10.6%), begging (4%), and eating discarded bait (10.6%). Ninety-seven percent of participating fishermen reported that king mackerel were taken by bottlenose dolphins. King mackerel was the species most often identified as being taken by bottlenose dolphins, but other fish reportedly taken included amberjack (*Seriola*

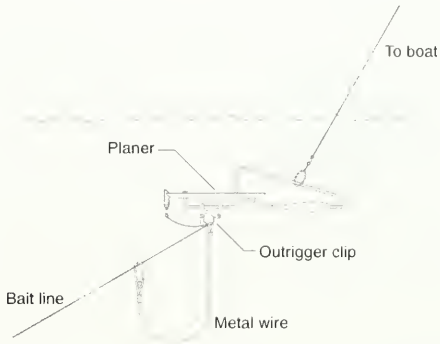

Figure 2

A device designed to reduce bottlenose dolphin (*Tursiops truncatus*) depredation in the commercial king mackerel (*Scomberomorus cavalla*) troll fishery. The device is created with an outrigger clip secured to the back of a planer. The wire, attached at one end to the outrigger clip and clipped at the other end to the bait line, is released from the outrigger clip when a fish bites the line, and it travels to the end of the bait line. At the end of the bait line, the metal wire flaps about and deters a dolphin from taking a captured fish. (Diagram by Eric Blankfield).

Table 1

Vessel type and location of respondents in interview surveys of fishermen for a study of bottlenose dolphin depredation in the Florida king mackerel fishery. Nine individuals selected more than one vessel type.

	Commercial	Charter	Recreational
Islamorada	1	23	3
East Coast	17	12	2

fasciata), blackfin tuna (*Thunnus atlanticus*), and Spanish mackerel (*Scomberomorus maculatus*) (Fig. 3).

More than half of the fishermen we interviewed indicated that the interactions with bottlenose dolphins occurred either daily or several times a week. In Islamorada, fishermen indicated that winter was the season with the highest number of interactions, and along the east coast of Florida, most interactions occurred during spring (Fig. 4). Most interviewees (76.6%) indicated they believed that bottlenose dolphin conflicts with fishing efforts had increased over the past several years. The vast majority (94%) of commercial fishermen indicated that bottlenose dolphin depredation was causing a significant economic loss, although a smaller number of charter fishermen held this view (Fig. 5). A Mann Whitney test indicated a significantly higher perceived economic loss from depredation for commercial fishermen than for charter fishermen ($P<0.001$).

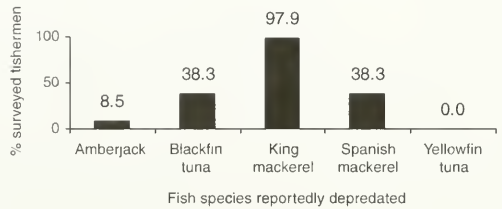

Figure 3

Percent of surveyed fishermen identifying fish species that are depredated by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) fishery. No individuals reported depredation of yellowfin tuna (*Thunnus albacares*), and all of the fishermen reported depredation of at least one of the listed fish species.

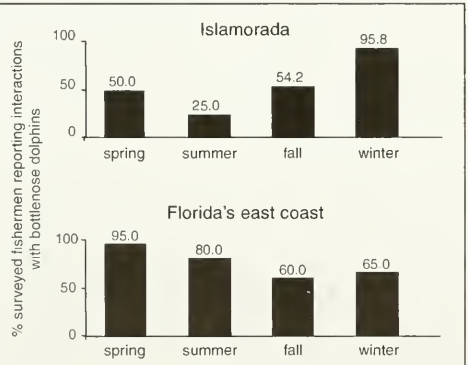

Figure 4

Percent of surveyed fishermen reporting interactions with bottlenose dolphins (*Tursiops truncatus*) during each season in the king mackerel (*Scomberomorus cavalla*) troll fishery along Florida's east coast and off Islamorada, Florida.

Observations of dolphins

We made observations from five charter boats in Islamorada and from four charter and four commercial boats along the east coast. We spent 41 hours conducting field observations in Islamorada and 85 hours along the east coast. We observed dolphins taking or attempting to take catch, following the boat, feeding or milling near boat with no interactions, and passing by the boat (Fig. 6). All the observations of bottlenose dolphins following the vessel occurred when the vessel was fishing for king mackerel.

We observed 15 fish taken or damaged by bottlenose dolphins. Depredation by bottlenose dolphins was characterized by an abnormal jerk on the line after a fish was known to have taken the bait. For charter fishermen, 6% of the king mackerel catches were taken or damaged by bottlenose dolphins. Depredation events occurred more frequently on commercial fishing vessels, where bottlenose dolphins took almost 20% of the king mackerel. We observed thirteen depredation events on commercial vessels and single depredation events while aboard charter vessels on Florida's east coast and off Islamorada. All depredation events occurred during fishing operations for king mackerel. Only one event occurred in Florida's state waters (within three nautical miles from shore); all others occurred between three and twelve nautical miles offshore. In both study areas, the number of dolphins observed while depredation occurred ranged from one to three dolphins, although other dolphins were often in the same area, following or engaging in depredation with nearby fishing vessels.

It proved impossible to photograph bottlenose dolphin dorsal fins during acts of depredation, because of the nature of the interaction. Bottlenose dolphins typically remained too far from the vessel to allow useful photographs to be obtained. When a fish was caught, the dolphins would swim rapidly towards the boat with their dorsal fins directly below the surface in order to take the fish. After taking the fish, the dolphins would surface well away from the boat.

Impact on the king mackerel fishery

During the fifteen depredation events, we observed lost and damaged fish and loss of gear, including line, lures, hooks, and occasionally planers. Fishermen typically responded to depredation by leaving the area or by ignoring the bottlenose dolphins. In one instance, we observed a charter boat captain shooting a gun into the water to protect his catch and fishing gear. We also observed the use of bird bangers, sound-creating devices similar to a

gun shooting blanks, in response to depredation. Anecdotal accounts of the use of seal bombs, guns, and bird bangers were also reported by commercial and charter fishermen.

Experimental testing of deterrence device

In three cases when the device was in use, bottlenose dolphins approached a king mackerel on the fishing line, but left the fish apparently after they detected the device. The number of fish caught per hour for each outrigger was 1.48. A *t*-test demonstrated no significant difference exists between the rate of fish caught by each outrigger when the device was not used (P=0.99). We also found no difference in the number of fish caught per hour by outriggers equipped with the device (1.40) with those without the device. The device did not cause a reduction in catch of targeted species (P=0.83).

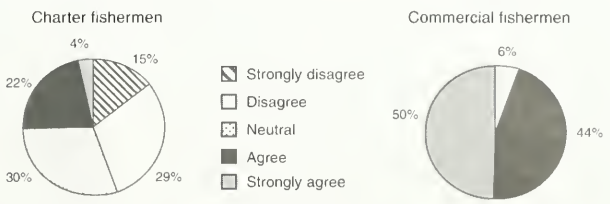

Figure 5

Response of surveyed fishermen when asked if they agree or disagree with the following statement: "bottlenose dolphins (*Tursiops truncatus*) are causing economic loss to my business by stealing bait and/or catch."

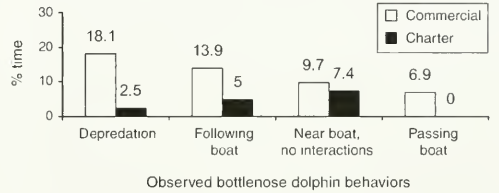

Figure 6

Bottlenose dolphin (*Tursiops truncatus*) behaviors observed from king mackerel (*Scomberomorus cavalla*) fishing vessels.

Discussion

We documented frequent depredation in both the king mackerel charter and commercial troll fisheries in southeastern Florida. All commercial and charter fishermen indicated that they experienced bottlenose dolphins taking their bait or catch. During our observations, approximately one in every five fish caught by commercial fishermen was lost to bottlenose dolphins, but only 6% of catch was lost by charter fishermen. This difference in depredation rates may be attributed to seasonal variation in the distribution of king mackerel or differences in the gear used by the two fishery sectors. Fishermen in Islamorada reported that most conflicts with dolphins occur in the winter. Because of the highly migratory nature of king mackerel and the mixing of the South Atlantic and Gulf stocks in the winter in the Florida Keys, we anticipated that a higher depredation rate would be experienced by the charter fishery in winter (Gold et al., 2002). We observed commercial fishing operations along Florida's east coast during the season with the most reported conflicts. Depredation rates along the east coast, however, may be even higher in the spring than at the end of spring and summer when our observations were made.

In addition, commercial fishermen target king mackerel, whereas charter boats use fishing gear that targets a variety of fish species, including amberjack, barracuda (*Sphyraena obtusata*), and bonito (*Sarda sarda*). The higher depredation rates encountered by commercial fishermen may result from the regular capture of king mackerel compared to the various species caught by charter boats during a fishing trip. In addition to king mackerel, species that were reported taken by both commercial and charter boat fishermen included Spanish mackerel, amberjack, and blackfin tuna. We did not observe depredation of these species, most likely because they were rarely caught during our study. However, depredation of these species has been reported from Spanish mackerel fisheries elsewhere (Read et al., 2003).

We observed bottlenose dolphins engaging in depredation only while the vessels were fishing for king mackerel. Bottlenose dolphins do not generally prey on king mackerel; Barros (1993) did not find king mackerel in the stomach contents of any stranded dolphins in Florida. Exploitation of fisheries by marine mammals may introduce a new food resource that was either not previously available or used, as seen in the case of pilot whales (*Globicephala spp.*) that feed on Atlantic mackerel (*Scomber scombrus*) in trawl fisheries off the northeastern United States (Waring et al., 1990; Gannon et al., 1997) and in the case of killer whales (*Orcinus orca*) that prey on swordfish (*Xiphias gladius*) hooked on longlines in southern Brazil (Secchi and Vaske, 1998). It is likely that fishing affects not only the diet but also the behavior and spatial distribution of bottlenose dolphins (Leatherwood, 1975; Chilvers et al., 2003). The bottlenose dolphins in this study may spend less time foraging, but as indicated by the observed depredation

of king mackerel, the diet and possibly the distribution of these animals is impacted by their interaction with the fishery.

In this study, fishermen reported observing female bottlenose dolphins "teaching" their calves how to engage in depredation, indicating a behavioral transmission of knowledge. Depredation of king mackerel by bottlenose dolphins may have resulted from a learned behavior that results in a low-cost foraging specialization.

Over three quarters of interviewed fishermen reported increasing conflicts with bottlenose dolphins. The frequency of these interactions most likely result from a combination of factors, including behavioral learning, increasing fishing effort, and spatial overlap and resource competition between cetaceans and fisheries (Donoghue et al.[2]). In addition, an upsurge in depredation may be correlated with a rise in troll fishing effort that resulted from the July 1995 statewide ban of gill nets in Florida (Wells et al., 1998). The increase in depredation places bottlenose dolphins in close proximity to fishing vessels and gear, increasing the risk of injury or death to the dolphins. It is unknown if the dolphins in this study were injured by hooks. Although we did not observe entanglement in this study, entanglement in and ingestion of fishing gear by bottlenose dolphins could result from depredation. Hucke-Gaete et al. (2004) observed a fatal entanglement of a sperm whale (*Physeter macrocephalus*), likely engaging in depredation, in a longline fishery off southern Chile. Monofilament fishing line does not degrade rapidly, and injury or death can result from the entanglement in or ingestion of fishing gear (Mann et al., 1995). Previous research has documented the deaths of bottlenose dolphins from entanglement (Wells et al., 1998) and from ingestion of monofilament line (Gorzelany, 1998).

As a result of lost or damaged gear and catch, fishermen experience economic loss from these interactions. Commercial fishermen reported significantly higher economic losses than charter boat fishermen. Our observations confirm the potential for high economic loss by commercial fishermen due to lost fishing gear and depredation. Because of the cost to commercial fishermen and risk to marine mammal safety, we investigated gear modification as a potential solution to reduce these conflicts (FR, 1996). Gear modification has proven successful in decreasing depredation and bottlenose dolphin mortality caused by entanglement in the blue crab fishery in Florida, in reducing seabird bycatch in coastal gillnet fisheries, and in reducing sea turtle entanglement in shrimp trawlers (Crowder et al., 1994; Melvin et al., 1999; Noke and Odell, 2002;). Our preliminary tests demonstrated that a modification to the outrigger planer will successfully deter bottlenose dolphins from engaging in depredation, without causing a reduction in catch. The deterrence device is made of fishing gear already owned by most fishermen and therefore the cost of the gear modification is minimal.

The deterrence device could prove beneficial in reducing fishery-related injury or mortality of bottlenose dolphins in the king mackerel troll fishery, including harm that may result from retaliatory measures of some fishermen. The 1994 amendments to the Marine Mammal Protection Act of 1972 allow the operator of a fishing vessel to deter a marine mammal from damaging his gear or catch. However, potentially harmful methods, such as guns and seal bombs observed and reported in the Florida king mackerel fishery, are strictly prohibited (FR, 1995). The deterrence device offers an alternative to such illegal measures and their associated harmful consequences. We recommend that the deterrence device be fully tested and, if successful, employed as a strategy to reduce depredation and its adverse effects on both fishermen and bottlenose dolphins.

Acknowledgments

We thank two anonymous reviewers who provided suggestions that improved this manuscript. Laura Engleby and the Dolphin Ecology Project provided housing and support that made this study possible. We acknowledge the Edna B. Sussman Fund and the Environmental Internship Fund at Duke University's Nicholas School of the Environment and Earth Science for providing funds to support this research and Steve McCulloch at Harbor Branch Oceanographic Institute for supplying housing on the east coast of Florida. Leigh Torres, Dave Johnston, Danielle Waples, and Kim Urian provided invaluable assistance with this study. We also thank Eric Blankfield who diagramed the fishing gear device. Finally, our appreciation goes to all participating fishermen.

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Reproductive biology, spawning season, and growth of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska

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Abstract—Rex sole (*Glyptocephalus zachirus*) have a wide distribution throughout the North Pacific, ranging from central Baja California to the western Bering Sea. Although rex sole are an important species in the commercial trawl fisheries off the U.S. West Coast, knowledge of their reproductive biology is limited to one study off the Oregon coast where ovaries were analyzed with gross anatomical methods. This study was initiated to determine reproductive and growth parameters specific to rex sole in the Gulf of Alaska (GOA) stock. Female rex sole (n=594) ranging in total length from 166 to 552 mm were collected opportunistically around Kodiak Island, Alaska, from February 2000 to October 2001. All ovaries were analyzed by using standard histological criteria to determine the maturity stage. Year-round sampling of rex sole ovaries confirmed that rex sole are batch spawners and have a protracted spawning season in the GOA that lasts at least eight months, from October to May; the duration of the spawning season and the months of spawning activity are different from those previously estimated.

Female rex sole in the GOA had an estimated length at 50% maturity (ML_{50}) of 352 mm, which is greater than the previously estimated ML_{50} at southern latitudes. The maximum age of collected female rex sole was 29 years, and the estimated age at 50% maturity (MA_{50}) in the GOA was 5.1 years. The von Bertalanffy growth model for rex sole in the GOA was significantly different from the previously estimated model for rex sole off the Oregon coast. This study indicated that there are higher growth rates for rex sole in the GOA than off the Oregon coast and that there are differences in length at maturity and similarity in age at maturity between the two regions.

Manuscript submitted 5 January 2005 to the Scientific Editor's Office.

Manuscript approved for publication 19 September 2005 by the Scientific Editor.

Fish. 104:350–359 (2006).

Rex sole (*Glyptocephalus zachirus*) have a wide distribution throughout the North Pacific, ranging from central Baja California to the western Bering Sea (Mecklenburg et al., 2002). The rex sole population is made up of several stocks that are managed as four separate units: the U.S. West Coast stock which includes waters off the coasts of California, Oregon, and Washington; the British Columbia stock which is managed separately by the Canadian government; the Gulf of Alaska (GOA) stock; and the Bering Sea stock (Turnock[1]). The U.S. West Coast stock of rex sole provided a steady and stable commercial fishery in California between 1970 and 1989, but landings began to decline in the 1990s (Quirollo and Dewees[2]). Rex sole are managed as part of the "other flatfish" category for both the West Coast stock (Quirollo and Dewees[2]) and the Bering Sea stock (Spencer et al.[3]).

Throughout its range, the largest commercial harvest of rex sole occurs in the GOA where rex sole are one of the major commercial flatfish species. Since 1988, the commercial trawl fishery for flatfish in the GOA has concentrated in the central Gulf on the continental shelf and slope east of Kodiak Island (DiCosimo and Kimball[4]). Development of a management plan for the rex sole fishery in the GOA has undergone several phases. Prior to 1990, all flatfishes in the GOA with the exception of Pacific halibut (*Hippoglossus stenolepis*) were managed as one assemblage. In 1990, four flatfish categories were created for stock assessment: shallow-water complex, deep-water complex (rex sole included), flathead sole (*Hippoglossoides elassodon*), and arrowtooth flounder (*Atheresthes stomias*). In 1993, rex sole were removed from the deep-water complex and managed as a separate species.

In 2003, biomass estimates for rex sole in the Gulf of Alaska totaled 99,950 metric tons (t), and the acceptable biological catch (ABC) was 9466 t (Turnock et al.[5]). Annual commercial landings for GOA rex sole averaged about 3000 t during 1999–2003, approximately 35% of the ABC (Turnock et al.[5]). The low harvest level may be due, in part, to constraints placed on

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the trawl flatfish fishery once the allowed limit of Pacific halibut bycatch is captured (DiCosimo and Kimball[4]).

The life history, reproductive biology, and growth of rex sole were investigated off the Oregon coast from 1969 to 1973 (Hosie and Horton, 1977). Despite the wide geographic range of rex sole, no investigations have occurred elsewhere. Although rex sole in the GOA are managed as a single species unit with species-specific assessments of biomass and ABC estimates, there is no information on length or age at maturity to incorporate into analytical stock assessments. Thus, there is a substantial need for obtaining information on the reproductive biology of rex sole in the GOA for the purpose of stock-specific assessment and management.

To clarify the seasonal maturation dynamics and reproductive biology of female rex sole in the GOA, fish were collected year-round and their ovaries were analyzed by using standard histological techniques. To date, there have been no histological investigations on rex sole maturity (Castillo, 1995). Specific goals of this investigation were to determine the spawning season, length at first maturity, length at 50% maturity (ML_{50}), age at first maturity, and age at 50% maturity (MA_{50}). Additionally, inasmuch as possible, reproductive parameters and growth were compared between female rex sole in the GOA with those off the Oregon coast (data from Hosie and Horton, 1977). Reproductive parameters determined in this study will aid the development of a species-specific assessment of target fishing mortality rates and mature female biomass, yielding a more accurate management model for the GOA stock of rex sole.

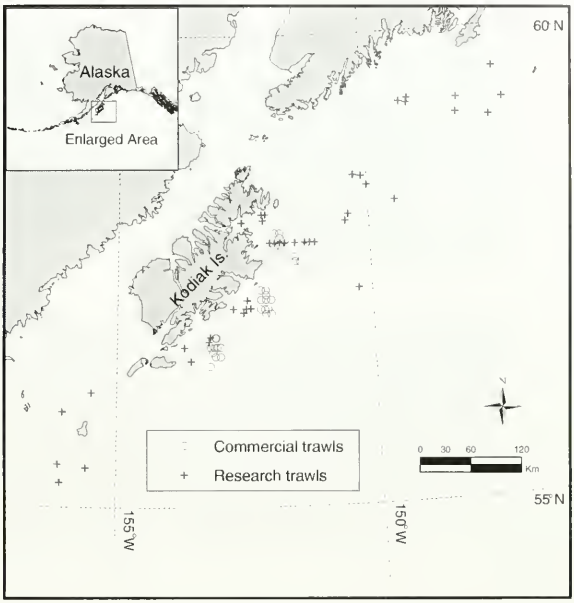

Figure 1

Collections of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska were concentrated around Kodiak Island, Alaska. Samples were obtained from the commercial trawl fishery (denoted by open circles) and from research survey trawls (denoted by crosses).

Materials and methods

Collections

Rex sole were collected from 14 February 2000 to 21 October 2001 in the central GOA (from 55°30′N, 156°00′W to 59°50′N, 147°15′W; Fig. 1). Approximately half (52%) of the samples were collected at fish processing plants in Kodiak, Alaska. The shore-side sampling data were dependent on the timing of the fishery, but allowed for the annual cycle of sexual maturation to be monitored. Shore-side sampling occurred in January, February, April, May, October, November, and December, and samples were obtained from boats that captured rex sole as bycatch while fishing for other species. Although there is no inherent biological difference in rex sole collected by commercial or research trawl, typically samples from the commercial fishery exclude young fish that are below the minimum landing size or escape through the meshes. However, because of the close proximity of the fishing grounds to the town of Kodiak, catches were not sorted at sea and very small rex sole (minimum total length [TL]=172 mm) were brought back to the processing plants where they were obtained for this study. The remaining 48% of samples were collected during research surveys in February, March, June, and July by the National Marine Fisheries Service (NMFS) and the University of Alaska Fairbanks with smaller-meshed trawls in the same waters fished by the commercial fishery.

Samples were stratified by length, so that up to five females per 1-cm length group were obtained each month. For each female, total length (to the nearest mm) and weight (to the nearest 0.1 gram) were measured, both sagittal otoliths were removed, and ovarian maturity was macroscopically staged. Each ovary was removed and weighed separately (to the nearest 0.1 gram). Ovaries were preserved in 10% buffered formalin for 2 months and then transferred to 70% ethanol. All ovaries collected at sea were weighed only after preservation; ovaries collected at processing plants were weighed both when fresh and after preservation.

Sagittal otoliths were removed from each fish, stored in a glycerol and thymol solution, and most (n=557)

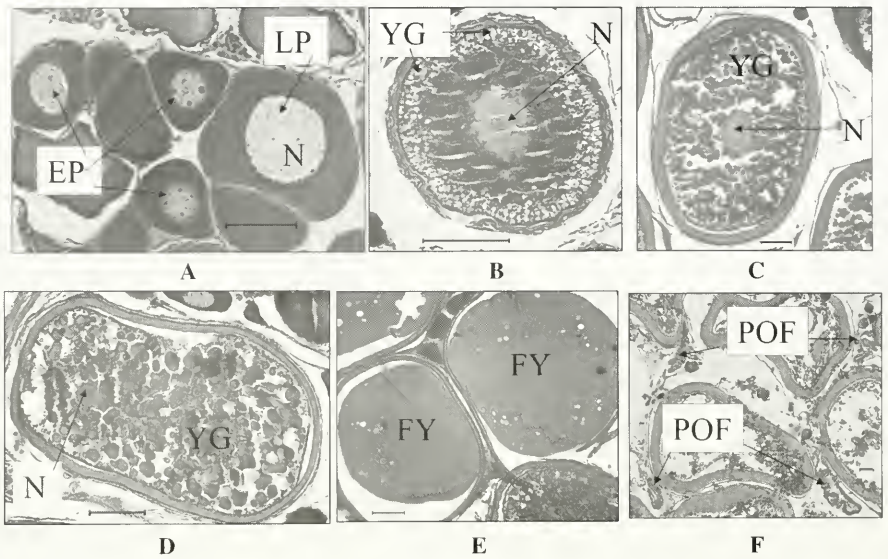

Figure 2

Photomicrographs of histological cross-sections of rex sole (*Glyptocephalus zachirus*) ovaries: (**A**) early perinuclear (EP) oocytes and late perinuclear [EP] oocytes, with a large central nucleus (N), that have not begun vitellogenesis; (**B**) early yolked oocyte beginning vitellogenesis with yolk globules (YG) at periphery of oocyte; (**C**) advanced yolked oocyte; (**D**) migratory-nucleus oocyte; (**E**) hydrated oocytes with fused yolk (FY); (**F**) postovulatory follicles (POFs). Each photomicrograph has a scale bar equal to 0.1 mm.

were analyzed for age determination. The left otolith, or blind-side otolith, was read because it is thicker along the proximal-distal axis, thereby allowing the annuli to be less compressed and easier to differentiate when counted from the core to the otolith edge along the sulcus (Anderl[6]). Otoliths were processed with standard break-and-burn techniques (Beamish and Chilton, 1982). Two experienced readers each read 117 otoliths and had initial agreement of 67%. The magnitude of the initial discrepancies within an age-group ranged from −2 to +3 years for females from age 2 to 18 years. All discrepancies of age estimates were resolved between readers through combined analysis. Once all discrepancies were resolved, the remaining otoliths were analyzed.

Histological analysis

Tissue from the middle portion of the right (ocular-side) ovary was embedded in paraffin Paraplast (McCormick Scientific, St. Louis, Missouri). Serial sections (5–8 microns thick) were prepared and stained with Harris hematoxylin (Sigma Aldrich, St. Louis, MO) followed by eosin counterstain (Sigma Aldrich, St. Louis, MO) (H&E). Each ovary section was examined for the presence or absence of the following oocyte stages (see Fig. 2): oocytes that had not begun vitellogenesis (early perinuclear [EP] and late perinuclear [LP]); oocytes in the first vitellogenic stages (early yolk [EY]); advanced yolked oocytes (AY); oocytes with a migratory-nucleus (MN); unovulated hydrated oocytes (HY); ovulated hydrated oocytes (ova); and postovulatory follicles (POF). During the initial stage of oocyte degeneration (known as alpha [α] atresia) the entire oocyte is resorbed by the hypertrophying granulosa cells of the follicle (Lasker, 1985). Presence of alpha atresia was noted for all histological stages of oocyte development, and the degree of alpha atresia in yolked oocytes was classified as either greater or less than 50% of all yolked oocytes in the ovary. The thickness of the ovarian wall was measured at five or more locations with an ocular micrometer.

Histological classification

Based on histological analysis, spawning categories were created for females (Table 1) according to the clas-

[6] Anderl, D. 2003. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Histological criteria for female rex sole (*Glyptocephalus zachirus*) reproductive state and maturity. Active female ovaries contained a sufficient number of advanced yolked oocytes for one spawning. Abbreviations are as follows: migratory-nucleus oocytes (MN), hydrated oocytes (HY), postovulatory follicles (POFs), oocyte stage present (+); oocyte stage absent (O); oocyte stage not considered (–), and either one or both oocyte stages present (>). A postspawning fish has totally spent ovaries.

Ovary activity	Maturity stage	Spawning condition	Unyolked oocytes	Early yolked oocytes	Advanced yolked oocytes	MN or HY oocytes	POFs	>50% yolked atresia	Number of fish in stage
Inactive	Immature	Nonspawning	+	O	O	O	O	–	274
Inactive	Mature	Nonspawning	–	+	O	O	O	–	44
Inactive	Mature	Nonspawning	–	–	+	–	O	+	0
Inactive	Mature	Postspawning	–	–	+	–	+	+	96
Active	Mature	Nonspawning	–	–	+	O	O	O	26
Active	Mature	Spawning	–	–	–	+	O	O	27
Inactive	Mature	Postspawning	–	–	O	O	+	–	14
Active	Mature	Spawning	–	–	>	>	+	O	113
Total									594

sification from Hunter et al. (1992). Females were first classed as active or inactive by using the following criteria. Through histological analysis, ovaries that contained a sufficient number of AY/MN/HY oocytes for one spawning were classed as active. Active females were then classed as either spawning or nonspawning. Ovaries without AY oocytes or with major atresia of AY oocytes were classed as inactive. Inactive females were first classed as nonspawning or postspawning and then inactive nonspawning females were further classed as mature or immature (Table 1). Active spawning females showed evidence of past spawning (POF present) or imminent spawning (MN or HY present), whereas active nonspawning females had no evidence of recent or imminent spawning but were presumed capable of spawning in the near future. Females with ovaries containing oocytes in early stages of vitellogenesis (EY oocytes present) were considered mature but inactive. Immature females had ovaries without vitellogenic oocytes.

The fraction of active females and the fraction of postspawning females was calculated for each month. The start of the spawning season was defined by the first observance of a hydrated oocyte or a POF and the end of the spawning season was defined when the last female with hydrated oocytes was observed. A one-way ANOVA was used to test for differences in the ovary wall thickness of mature females among months. Assumptions of homogeneity of variances and normal distribution of observations were met for the ANOVAs. Bonferroni all-pairwise multiple comparison tests were used after the ANOVAs to test for differences among monthly mean values. Alpha was set at 0.05 for all tests of significance.

To estimate the length and age at which 50% of the female rex sole were mature ($ML_{50}$and MA_{50}), I used the logistic regression model:

$$Pmat = 1 / (1 + e^{a+bL}),$$

where $Pmat$ = the fraction of mature females per 15-mm length-class; and

L = total length in millimeters.

Similarly, for estimating MA_{50},age (in years) was substituted for length in the above equation. In each case, the equation was solved for $Pmat = 0.5$ to obtain the length and age at 50% maturity. The equation for the upper and lower 95% confidence limits around $Pmat$ when $Pmat = 0.5$ was solved to yield 95% confidence limits around $ML_{50}$and MA_{50}. Results were compared with existing length-at-maturity data for female rex sole off the Oregon coast by reconstructing a length-at-maturity logistic regression model from data presented by Hosie and Horton (1977), taking the log transformation of both the GOA and Oregon logistic regression curves to make them linear, and then comparing the slopes of the two lines according to Zar (1999). Direct statistical comparison with existing age-at-maturity data (e.g., the age at 50% maturity, and age at 100% maturity) for female rex sole off Oregon (Hosie and Horton, 1977) was not conducted because Hosie and Horton (1977) did not present standard error or logistic regression equations. Instead, the probability that a specific-size (or specific-age) female rex sole off the coast of Oregon would be considered mature in the GOA was calculated as the fraction of mature GOA females of the specified length divided by the GOA sample size of the specified length (Zar, 1999).

Size and growth

The relationship between weight and length for female rex sole in the GOA was estimated with the equation

$$W = aL^b,$$

where W = the total fish weight in grams; and
L = total length in cm.

This relationship was also determined for ovary-free weight. Because fresh ovarian weights were not measured for samples collected at sea, the fresh weight was estimated from a linear regression between fresh and preserved weights from the samples collected at processing plants. The linear regression OW=1.127 (OW_f)−0.024 was used to convert formalin-preserved ovary weights, OW_f, to estimates of fresh ovary weights, OW (n=446, r^2=0.997, P<0.0001). When fresh and preserved ovary weights differed; fresh ovaries usually weighed more than ovaries preserved in formalin, and the maximum difference between fresh ovaries and formalin-preserved ovaries was 20%.

Parameters of the von Bertalanffy growth model (L_∞, k, and t_0) were estimated for female rex sole in the GOA by using nonlinear least squares regression with the equation

$$L_t = L_\infty (1 - e^{-k(t - t_0)}),$$

where L_t is length at age t.

All length and age data were used for the GOA growth model. Statistical comparison of growth rates for female rex sole in the GOA with those from the Oregon coast were less rigorous because Hosie and Horton (1977) used mean values of length at age to calculate the von Bertalanffy growth model, thereby decreasing the variability in length at age, which was not presented. Therefore, the parameters L_∞, k, and t_0 in the GOA growth model were each statistically compared with the parameters in the Oregon growth model for females age 1–15 years (data from Hosie and Horton, 1977) with three separate Z-tests (Zar, 1999). Alpha was set at 0.05 for all tests of significance.

Results

Maturity

Oocyte development and maturity stage were determined for 594 female rex sole. Histological examination revealed that 46% of the collected females were immature and 54% were mature. Both immature and mature females were collected in every month; however, no fish were sampled in August or September (Table 2). Year-round histological analysis of ovaries confirmed that rex sole are batch spawners, as seen in the presence of POFs, features associated with recent spawning, concurrent with advanced vitellogenic oocytes.

The spawning season of rex sole in the GOA was protracted; postovulatory follicles first appeared in October and hydrated oocytes occurred as late as May, indicating a spawning season that spans at least eight months. Active females were present from October through May and were absent in June and July (Table 2). Mature postspawning females with no healthy AY oocytes first appeared in April and increased in June and July; thus, the spawning season ended in April for some individuals, and by June all rex sole had completed spawning (Fig. 3). The high number of postspawning fish combined with the absence of spawning fish in June and July indicated that the duration of POFs in an ovary was several weeks. Active females had at least one of the following oocytes (AY, MN, or HY) and could have any combination of these advanced stage oocytes, or all three oocyte stages at once. These oocytes were large and stretched the ovary wall quite thin, whereas inactive postspawning females had shrunken ovaries and thicker ovary walls (Maddock and Burton, 1999). In May and July ovary walls in mature females were significantly thicker than in all other months sampled (ANOVA: $F_{9,274}$=28.64, P<0.0001; Fig. 4), corresponding to the high fraction of postspawning females present from May to July (Table 2, Fig. 3).

Female rex sole sampled for length and maturity ranged from 166 to 552 mm TL (Fig. 5). The smallest

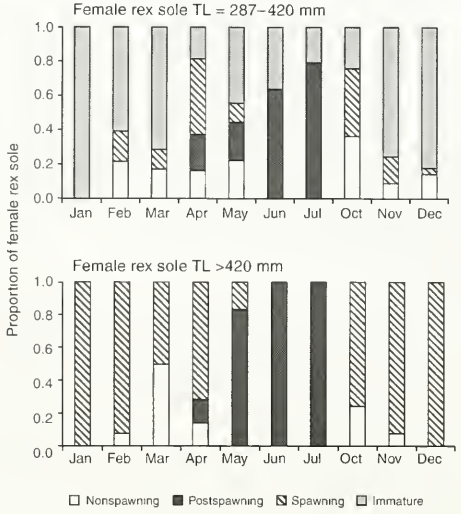

Figure 3

Monthly proportion of female rex sole (*Glyptocephalus zachirus*) maturity stages graphed separately for fish greater than size at first maturity (287–420 mm in upper graph) and fish greater than size at 100% maturity (>420 mm in lower graph). No data were collected in August or September. All mature rex sole were in the postspawning stage in June and July.

Table 2

Numbers of female rex sole (*Glyptocephalus zachirus*) in various histological subclasses, listed by month with years combined. Abbreviations are as follows: postspawning (PS), nonspawning (NS), spawning (S), early yolked oocytes (EY), advanced yolked oocytes (AY), migratory nucleus oocytes (MN), and hydrated oocytes (HY). Mature PS females had ovaries that contained post-ovulatory follicles (POF), and mature S females had ovaries that contained either MN or HY oocytes or AY oocytes combined with POF. The length distribution (minimum, maximum) and the total number of females sampled in each month are given. The percent active females in each month is given, and female rex sole were active from October through May. PS females were present from April to July. No collections were made in August or September.

Ovary activity	Maturity stage	Histological criteria	Jan	Feb	Mar	Apr	May	Jun	Jul	Oct	Nov	Dec	Total
Inactive	Immature	Unyolked oocytes	2	75	33	20	13	14	36	10	41	30	274
	Mature	EY; <50 % atresia	0	13	10	8	2	0	0	6	1	4	44
	Mature–PS	AY; >50 % atresia; POF	0	0	0	9	6	37	44	0	0	0	96
	Mature–PS	AY absent; POF	0	0	0	1	1	0	12	0	0	0	14
Active	Mature–NS	AY; POF absent	0	5	2	0	0	0	0	15	4	0	26
	Mature–S	MN or HY; POF absent	0	0	0	0	0	0	0	23	3	1	27
	Mature–S	AY, MN, or HY; POF present	5	37	10	24	2	0	0	18	16	1	113
Minimum length (mm)				353	166	250	214	215	257	176	267	172	220
Maximum length (mm)				513	529	552	547	460	503	450	476	460	452
Percent active females			71%	32%	22%	39%	8%	0	0	78%	35%	6%	
Percent postspawning females			0	0	0	16%	29%	73%	61%	0	0	0	
Total number sampled			7	130	55	62	24	51	92	72	65	36	594

mature female in the GOA was 287 mm TL. The nonlinear logistic regression model used to determine a length-at-maturity curve for females in the GOA had a very good fit (n=594, r^2=0.994; Fig. 6). The ML_{50} estimate for rex sole in the GOA was 352 mm (95% CI: 344–360 mm; Table 3), and length at 100% maturity was 420 mm (Fig. 5). Female rex sole in the GOA matured at a significantly larger size than off the Oregon coast (slope comparison: $t_{2,57}$=1356, P<0.0001; Fig. 6). Hosie and Horton (1977) estimated the ML_{50} as 24 cm off the Oregon coast, and at this length no GOA rex sole were mature. At the length that 100% of rex sole from Oregon waters were mature (30 cm; Hosie and Horton, 1977), only 15.8% (n=19) were mature in the GOA. The ML_{50} for female rex sole in the GOA was 46% greater than the ML_{50} for Oregon coast stock.

Female rex sole collected in this study ranged in age from 1 to 29 years. The estimated MA_{50} was 5.1 years (95% CI: 4.7–5.5 years) (n=557, r^2=0.988; Table 3, Fig. 7). Minimum age-at-maturity was 3 years, and all females had reached maturity by age 9, with the exception of two slow growing females who were still immature at ages 9 and 10 years (Fig. 5). These results are nearly identical to those obtained in Oregon (MA_{50}=5 yr, 100% mature at 9 years.; Hosie and Horton, 1977).

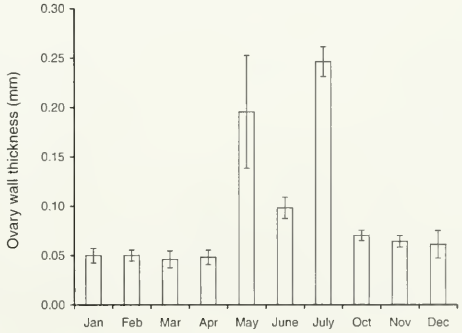

Figure 4

Monthly mean (±1 standard error) ovarian wall thickness (mm) for mature female rex sole (*Glyptocephalus zachirus*). No data were collected in August or September.

Size and growth

Parameters for the weight (g) to total length (cm) relationship for female rex sole in the GOA were

$W=0.000762L^{3.6127}$ ($n=573$, $r^2=0.963$, $P<0.0001$). Parameters for the ovary-free weight to total length (cm) relationship were $W=0.001277L^{3.4680}$ ($n=568$, $r^2=0.969$, $P<0.0001$). Parameters of the von Bertalanffy growth model for female rex sole in the GOA were $L_\infty=41.824$, $k=0.388$, and $t_0=-0.022$ ($n=556$, $r^2=0.480$, $P<0.0001$). All GOA parameters of the von Bertalanffy growth model differed from those off the coast of Oregon: L_∞ ($Z=8.01$, $P<0.0001$), k ($Z=5.61$, $P<0.0001$), and t_0 ($Z=2.29$, $P=0.0110$). Female rex sole age 1–15 years grew much more quickly in the GOA than off the Oregon coast (Fig. 8).

Discussion

A representative sample of fish can be challenging to collect during the spawning season, because samples from spawning aggregations may produce disproportionately large numbers of mature fish whereas samples from elsewhere may yield unusually large numbers of immature fish (Sampson and Al-Jufaily, 1999). The combination of samples from commercial trawls and randomly chosen trawls taken on research surveys provide a reasonable representation of the GOA population and are suitable for estimating spawning season, length and age at maturity, and growth rate. Shore-side sampling of the commercial catch enabled the annual cycle of rex sole sexual maturation to be monitored, and although a common problem in obtaining samples from commercial fishing gear is that the size-selectivity of trawls may produce biased estimates of size frequency and size at age (Sampson and Al-Jufaily, 1999), this concern was alleviated because small rex sole (minimum length=172 mm) were collected from processing plants.

One limitation in the sampling effort was that samples could not be obtained in August and September. This raises two concerns. First, the onset of the GOA spawning season was estimated to be October by the presence of POFs in mature ovaries; but, in all probability, it may begin earlier. Second, Hunter et al. (1992) argue that length and age at maturity are best estimated from fish collected prior to the spawning season, because during the spawning season the ovaries of some postspawning females are reabsorbed to the extent that they are indistinguishable from those of immature females. Their estimates of Dover sole (*Microstomus pacificus*) length at maturity from samples taken during the spawning season were 1.6–5.7 cm higher than estimates from samples taken prior to the onset of spawning (Hunter et al., 1992). Given that GOA collections were unavailable prior to the spawning season, estimates of ML_{50} in the present study may have been biased high. However, because 1) all postspawning females had POFs present and 2) there were no females that had atretic yolked oocytes without POFs, it is unlikely that mature females were misclassified as immature in this study.

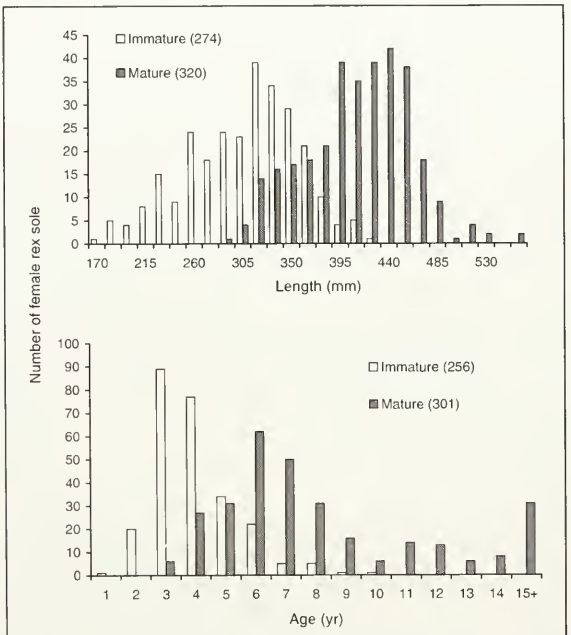

Figure 5

The number of immature and mature female rex sole (*Glyptocephalus zachirus*) by total length (upper graph) and age (lower graph). Sample size is given in parentheses. Lengths are binned at 15-mm increments and "age 15+" includes all females from 15 to 29 years old. Minimum size at maturity occurred in a fish with total length of 287 mm, and minimum age at maturity occurred at 3 years.

Spawning season

The spawning season for the population of female rex sole in the GOA ends in May and appears to commence in October, although it may begin earlier (see above). Castillo (1995) estimated the spawning season for rex sole in the GOA lasts from April through September, which differs markedly from results in the present study which are based on year-round histological examination of ovaries. Castillo (1995) based his estimation on the seasonal occurrence of rex sole larvae near Kodiak Island (Kendall and Dunn, 1985) rather than on collections of adult rex sole in spawning condition. Because rex sole larvae attain an exceptionally large size (up to 89 mm standard length) and have a prolonged pelagic life of

Table 3

Logistic regression model for female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska: final maturity thresholds, length and age at 50% maturity (ML_{50} and MA_{50}), sample size (n), model parameter estimates, and the model r^2.

Variable	ML_{50}/MA_{50}	95% CI	n	a	SE	b	SE	Model r^2
Length (mm)	351.7	343.7–359.7	594	13.79	0.77	−0.0392	0.0022	0.994
Age (years)	5.1	4.7–5.5	557	5.29	0.45	−1.0375	0.0854	0.988

at least 12 months (Pearcy et al., 1977), the indeterminate pelagic larval phase may have confounded Castillo's (1995) estimates.

Fish may adjust their spawning season to synchronize larval hatching date with the season that is most favorable for larval feeding (Qasim, 1956). Because primary production at northern latitudes is restricted to a short, intense period during early summer, fishes at higher latitudes often delay and shorten their breeding season as an adaptation to synchronize the feeding of fish larvae with the zooplankton bloom (references in Qasim, 1956; Castillo, 1995). However, rex sole in the GOA spawn earlier in the year and for a longer duration than those off the Oregon coast, which spawn from January to June (Hosie and Horton, 1977). Hence, rex sole do not fit the typical pattern of geographic variation found in other pleuronectids, such as English sole (*Pleuronectes vetulus*; Kruse and Tyler, 1983; Sampson and Al-Jufaily, 1999), Dover sole (Abookire and Macewicz, 2003), and yellowtail flounder (*Limanda ferruginea*; Zamarro, 1991).

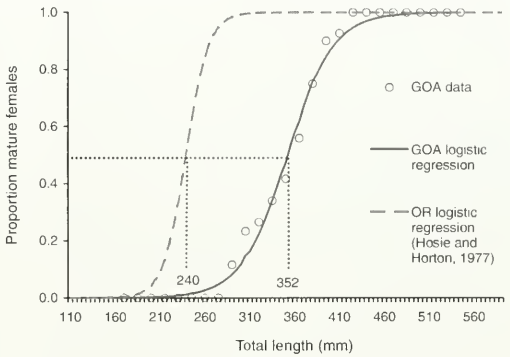

Figure 6

Proportion of female rex sole (*Glyptocephalus zachirus*) that were sexually mature in the Gulf of Alaska (GOA) as a function of total length (mm). Data points along the GOA curve represent the proportion of mature females in each 15-mm length-class interval. Logistic model parameter estimates are listed in Table 3. The dashed line denotes the length at which 50% of females are mature, and the actual size (mm) of ML_{50} is given. A maturity curve for female rex sole off the Oregon (OR) coast (from Hosie and Horton, 1977) is graphed for comparison. Female rex sole in the GOA mature at a significantly larger size than off the Oregon coast ($P<0.0001$).

Maturity and growth

Size and age at sexual maturity are two important parameters of fish stock assessment models used to estimate spawning biomass and annual catch quotas, but these parameters may vary throughout the geographic distribution of a species (Roff, 1981; Nichol, 1997; Bromley, 2000) and can be influenced by food availability (Castillo, 1995; Sampson and Al-Jufaily, 1999), oceanographic conditions (Kruse and Tyler, 1983; Brodziak and Mikus, 2000), or population size (Morgan and Colbourne, 1999). Along the west coast of North America both English sole (Sampson and Al-Jufaily, 1999) and Dover sole (Brodziak and Mikus, 2000; Abookire and Macewicz, 2003) exhibit geographic variation in length at maturity and growth.

There is some indication that female rex sole mature at a smaller size in the southern portion of their range: off San Francisco, California, females were fully mature at 22.8 cm (in Hosie and Horton, 1977), and off the Oregon coast ML_{50} was 24 cm (Hosie and Horton,

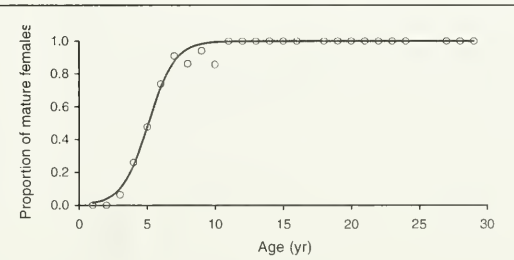

Figure 7

Proportion of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska that were sexually mature as a function of age (years). Datapoints along the curve represent females grouped in intervals of one year. Logistic model parameter estimates are listed in Table 3.

1977). Correspondingly, I found the ML_{50} in the GOA (35 cm) was 46% greater than that off the Oregon coast. Although there is a possibility that rex sole ML_{50} in the GOA was overestimated because sampling did not occur prior to the onset of spawning, the bias cited by Hunter et al. (1992) was relatively small and can not fully account for the 11 cm difference in ML_{50} between the GOA and Oregon. However, some caution must be exercised when maturity is compared between the GOA and Oregon (Hosie and Horton, 1977) because about 25 years elapsed between studies and different criteria were used to classify fish as mature.

Differences in the histological criteria used to define mature individuals and reliance solely on gross anatomical methods can lead to a misclassification of maturity and produce differences in estimates of ML_{50} (Hunter et al., 1992; Zimmermann, 1997). In a comparison of histological and gross anatomical methods, Hunter et al. (1992) found 1% of active female Dover sole were misclassified as inactive and 12% were visually classified as having advanced yolked oocytes and believed capable of spawning, whereas histological analysis indicated that they were inactive and future spawning was unlikely. Likewise, macroscopic examination of arrowtooth flounder misclassified 18.4% of maturing or spent females as immature and 4.4% of immature females as spent (Zimmermann, 1997). Unfortunately, in the only previous investigation on rex sole maturity, Hosie and Horton (1977) limited their analysis of ovaries to macroscopic staging. However, the enormous differences in ML_{50} between the GOA stock and the West Coast stock off Oregon likely stem from biological differences between stocks rather than from inconsistent methods used in the two studies. This interpretation is consistent with the dramatic difference in length at age between the two areas (Fig. 8) that was demonstrated in this study.

Given that Hosie and Horton (1977) used the otolith-surface aging technique to analyze rex sole otoliths, they may have underestimated ages and thereby biased their estimates of both age at maturity and growth rates. However, the tendency to underestimate age with the otolith-surface aging technique is greater for older fish where the outer edges of the otolith are worn (Anderl[7]). Surface analysis of several GOA rex sole otoliths revealed that, although break and burn is the preferred technique for aging rex sole otoliths, it is possible, depending on the clarity of the annular pattern, to age females less than 10 years old accurately by using otolith surfaces (Anderl[7]). Because the ages at 50% and 100% maturity off the Oregon coast were 5 and 9 years old, respectively (Hosie and Horton. 1977), there is a lower potential for bias caused by the surface aging technique because fish were <10 years old. Although these different aging methods may limit comparisons of age at maturity, the similarity in age

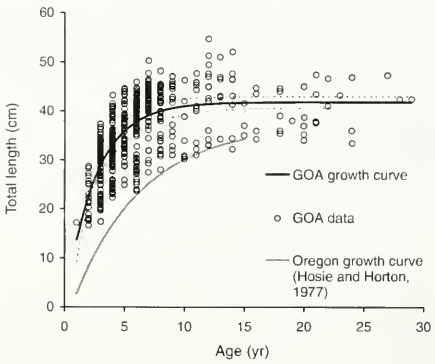

Figure 8

The von Bertalanffy growth curve with 95% confidence limits for female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska. Parameters of the Gulf of Alaska growth model were $L_\infty = 41.82$, $k = 0.388$, and $t_0 = -0.022$. For comparison, the growth curve for age 1–15 female rex sole off the Oregon coast is graphed with data from Hosie and Horton (1977).

at maturity between the GOA and Oregon is strongly indicated. Additionally, because the length-at-age data presented in growth curves from Oregon were only for rex sole <15 years old (Hosie and Horton, 1977), and a difference in growth is evident at young ages (Fig. 8), it seems unlikely that potential bias from otolith-surface aging methods—rather than from biological differences between stocks—could account for the markedly lower growth rate of Oregon rex sole. To be sure, it would be useful for future research to compare the reproductive biology and growth data of female rex sole in the GOA with a current study off the Oregon coast that employed similar aging techniques and histological criteria for maturity to determine if the distinct differences found in the GOA stock (i.e., larger size at maturity, similar age at maturity, faster growth rate) persist.

Acknowledgments

Sampling was a cooperative effort and fish were collected with the assistance of National Marine Fisheries Service, University of Alaska Fairbanks School of Fisheries and Ocean Sciences, and Kodiak Island processing plants (Trident Seafoods, Alaska Pacific Seafood, and Cook Inlet Processing). I especially thank A. Barns, D. Benjamin, E. Brown, H. Emberton, R. Foy, B. Holladay, and N. Raring. I am grateful for the histology advice from D. Nichol and B. Macewicz, and statistical advice from M. Litzow. I thank E. Acuna for preparing slides, and I thank D. Anderl, J. Lyons, and R. Katona

[7] Anderl, D. 2004. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

from the Age and Growth Unit of the Alaska Fisheries Science Center for aging otoliths. I thank M. Litzow, D. Nichol, D. Somerton, B.J. Turnock, M. Wilkins, and two anonymous reviewers for providing critical reviews of the manuscript. Project funding was provided by the Resource Assessment and Conservation Engineering Division of the Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration.

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How much does the fishery at Apo Island benefit from spillover of adult fish from the adjacent marine reserve?

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Abstract—The contribution of the no-take marine reserve at Apo Island, Philippines, to local fishery yield through "spillover" (net export of adult fish) was estimated. Spatial patterns of fishing effort, yield, and catch rates around Apo Island were documented daily in 2003–2004. Catch rates were higher near the reserve (by a factor of 1.1 to 2.0), but fishing effort was often lowest there. Higher catch rates near the reserve were more likely due to spillover than to low fishing intensity. Lower fishing effort near the reserve may have been due to 1) weather patterns, 2) traditional importance of other fishing grounds, 3) high variability in catch rates, 4) lower market value of target species, and 5) social pressures. The yield taken near the reserve was only 10% of the total yield, but the actual spillover contribution was probably much less than this. This study is one of the few to estimate the spillover contribution to overall yield and to document the responses of fishermen to spillover.

Manuscript submitted 5 November 2004 to the Scientific Editor's Office.

Manuscript approved for publication 20 September 2005 by the Scientific Editor.

Fish. Bull. 104:360–375 (2006).

No-take marine reserves (areas closed to fishing) are now often established with an objective of sustaining or enhancing fisheries (Gell and Roberts, 2003). Reserves could achieve such objectives by eventually becoming net exporters of adult biomass, defined as "spillover," and by providing net larval export, known as the "recruitment effect" (Russ, 2002). Fisheries will probably benefit from spillover in a minor way only. Theoretical studies have indicated that potential fishery yield (yield per recruit) from spillover would be insignificant, if any yield at all, except when stock abundance outside reserves is very low due to high fishing mortality (Polacheck, 1990; Russ et al., 1992; DeMartini, 1993). Thus, potential gains from spillover are predicted to be only moderate. There seems to be general agreement that the more important fishery enhancement effect of reserves would be due to net larval export (Carr and Reed, 1993; Russ, 2002). However, the establishment of reserves, particularly in developing countries, requires strong support from local stakeholders, especially fishermen (Russ and Alcala, 1996; Galal et al., 2002). There is a concern that, in some cases, support for reserves may be difficult to obtain on the pretext of enhanced fisheries through increased recruitment (Russ and Alcala, 1996). Net larval export may seem less convincing to fishermen because of the broad spatial scale (tens to hundreds of kilometers) at which it will probably occur (Russ and Alcala, 1996; Russ, 2002). Yields from spillover, although probably small, may play a critical role in convincing fishermen to support establishment and maintenance of reserves (Russ and Alcala, 1996). For some fishermen, adult fish "spilling-over" from reserves, especially in the case of larger fish, will appear to be a more direct and tangible benefit than larvae recruiting to fishing grounds from distant reserves. Thus, spillover may have a substantial positive psychological effect on the attitudes of fishermen toward reserves.

However, few empirical studies have quantified the effects of spillover on fishery yields, nor the responses of fishermen to spillover, perhaps because some advocates of reserves are sometimes overly optimistic about the potential benefits of spillover. Two studies in one location in Kenya showed that after several years of reserve protection, spillover was not enough to compensate for reduction of total yield due to the creation of a large no-take reserve (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000). The reserve, Mombasa Marine Park, took away 50–60% (~6–8 km^2) of the total fishing area. In this case the reserve probably occupied too large an area to supplement total fishery yield substantially (McClanahan and Mangi, 2000). However, in other countries, no-take reserves as large as Mombasa

Marine Park are rare. In the Philippines, for example, reserves that are created with fishery enhancement as a major goal are typically small (<1 km^2 of reef area) and occupy ≤25% of the available local fishing area (Alino et al., 2002). To date, only two studies of Philippine reserves, Sumilon and Apo (~25% and ~10% respectively of fishing area are no-take reserves), have shown persuasively that spillover yield may affect total fishery yield (Alcala and Russ, 1990; Russ et al., 2004, Alcala et al., 2005). In both cases, however, the magnitude of actual spillover yield was unclear (Russ et al., 2004, Alcala et al., 2005). On the other hand, two studies, one in St. Lucia (Roberts et al., 2001) and one in Egypt (Galal et al., 2002), demonstrated that catch rates of fishermen increased several years after the creation of networks of reserves. It was argued in these studies that the reserves increased total fishery yield because catch rates improved but fishing effort remained constant. However, these studies provided no information on total fishery yield, precluding estimation of the magnitude of spillover benefits. More empirical studies are needed to provide assessment of potential spillover effects on adjacent fisheries.

Besides available fishing area, the total fishery yield for a given location will be determined by fishing intensity (Hilborn and Walters, 1992). In addition, theoretical studies indicate that spillover yield will be a function of reserve size, fishing mortality rate, and demographic parameters of target species, particularly movement rates (Polacheck, 1990; Russ et al. 1992; DeMartini, 1993). However, the actual contribution of spillover to total yield will be determined by fishing intensity adjacent to reserves. Indeed it has been suggested that the "first" sign of spillover is the sight of fishermen fishing close to reserve boundaries (Gell and Roberts, 2003). This phenomenon would occur presumably in response to higher catch rates near than far from reserves. Spillover is predicted to produce a pattern of higher abundance of target species outside but close to reserve boundaries, but lower abundance farther away (Rakitin and Kramer, 1996; Kramer and Chapman, 1999). Decreasing catch rates (an index of abundance) away from reserve boundaries have been demonstrated by experimental trap fishing outside one reserve in Barbados and one reserve in Kenya (Rakitin and Kramer, 1996; McClanahan and Mangi, 2000). Also, monitoring studies of reserves in Kenya and the Philippines have shown that catch rates of fishermen were higher closer to reserve boundaries than farther away (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000; Russ et al., 2003, 2004). In New Zealand, large catches of lobsters were found to be more common closer to Leigh Marine Reserve than farther away (Kelly et al., 2002). However, it is less clear if fishermen tend to concentrate more effort adjacent to reserves when spillover may be present. Some studies suggest that fishermen may do so (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000), whereas other studies indicate that fishermen do not (Russ et al., 2003; Wilcox and Pomeroy, 2003). Some of the evidence for fishermen preferentially fishing near reserves is anecdotal (Gell and Roberts[1]). Nevertheless, it is important to stress that intense fishing near the reserve may have the effect of eventually reducing catch rates there (McClanahan and Mangi, 2000).

Fishing effort may not necessarily track the spatial distribution of fish abundance. Fishermen may not favor fishing adjacent to reserves even if catch rates there are higher. Catch rates alone may not explain the spatial distribution of fishing effort, because decisions by fishermen on where to fish are usually aimed at making a profit. Hence, decisions may be influenced by fishing costs, such as fuel or time used traveling to fishing areas (Hilborn and Walters, 1992). These costs will be related to the distance of fishing grounds from home ports or residences of fishermen (e.g., Wilcox and Pomeroy, 2003). If such costs are negligible, then fishing effort may reflect the spatial pattern of catch rates, provided that fishermen have ample information on the latter. However, this situation may be unlikely if fishermen keep information about productive areas to themselves. Furthermore, the strategies of fishermen may become highly complex in fisheries that employ a variety of fishing gears and target a multitude of species (Hilborn and Walters, 1992). This is likely to be particularly true of coral reef fisheries in developing countries (Munro, 1996). Spatial distribution of fishing effort in such fisheries may also depend upon the differential value of target species. In addition, other factors that are unrelated to income may also influence the spatial pattern of fishing effort. These include weather conditions and social factors, such as local traditions or agreements among stakeholders and managers (Wilcox and Pomeroy, 2003). Consideration of the behavior of fishermen in relation to reserves may help determine if reserves are achieving their goal of improving fishery yields through spillover. Successful use of reserves to enhance fisheries would require a case by case understanding of the spatial structure of impacted fisheries, ecosystems, and human communities (Hilborn et al., 2004).

The objective of this study was to estimate the upper limit of the spillover contribution of the no-take reserve at Apo Island, Philippines to the local fishery yield. The reserve at Apo Island has been protected for over 20 years (since 1982), and there is evidence to suggest that spillover is present (Russ and Alcala, 1996; Russ et al., 2003, 2004; Alcala et al., 2005). However, previous studies indicate that access by fishermen to productive areas far from the reserve during favorable weather influences the local fishery yield considerably (White and Savina, 1987; Bellwood, 1988). In the present study, daily fishing effort and yield were documented for eight months covering two monsoonal seasons. Spatial and temporal patterns of fishing effort, yield (biomass and value), and catch rates were examined among fishing

[1] Gell, F., and C. M. Roberts. 2002. Unpubl. report. The fishery effects of marine reserves and fishery closures, 89 p. WWF-US, 1250 24th Street. NW, Washington D.C. 20037.

grounds around Apo island and within a few hundred meters of reserve boundaries.

Materials and methods

Study site

Apo Island (9°4'N, 123°17'E) is located in the central Philippines, about 7 km southeast of the large island of Negros (Fig. 1). It is a small volcanic island with a fringing reef area of 1.06 km^2 to the 60-m isobath (0.54 km^2 to the 20-m isobath). The island is inhabited by a community of about 700 permanent residents. The traditional source of income for the community is fisheries. At present, about 100 residents are full-time or part-time fishermen who use hook and line, gill nets, spear guns, and fish traps, and target at least 60 species of reef fishes, nonreef fishes, and some invertebrates. The majority of local fishermen sell their catch to resident fish buyers on Apo Island. Fish buyers, in turn, bring the catch to Negros to sell in Malatapay town or Dumaguete City.

In 1982, a ~450 m long no-take reserve (sanctuary) was established informally by the local community on the southeastern side of Apo Island (Fig. 1). This reserve occupies approximately 10% of the fringing reef area to the 60-m isobath (about 13% to the 20-m isobath). The local community has effectively enforced protection of the no-take reserve since 1982 (Russ and Alcala, 1999). In 1985–86, the community formally approved a marine management plan that incorporated the no-take reserve (Russ and Alcala, 1999; White et al., 2002). The management plan also prohibited destructive fishing methods (e.g., dynamite fishing and muro-ami drive-net fishing) and spear fishing with SCUBA. Compliance by local fishermen and visitors with these regulations has been generally good. Development of local tourism enterprises has been encouraged by the Marine Management Plan. In the early to mid-1990s, two small resorts that could accommodate recreational SCUBA divers were established on Apo Island. Recently, the local community implemented collection of fees for diving in the no-take reserve and at dive sites around the island.

Apo Island is influenced by a northerly mainstream current that is present for most of the year (Fig. 1). This current presumably carries the food supporting planktivorous fishes (e.g., Acanthuridae and Caesionidae) that are abundant on the northern side of the island. Predatory fishes such as Carangidae are also common in this area. Apo Island is exposed to both the NE and SW monsoons (Fig. 1). Local fishermen tend to fish the northern side of the island during the SW monsoon (June to September) and interim calm months (April, May, and October; Bellwood, 1988). However, fishing intensity on the northern side of the island may be reduced during the NE monsoon (November to March; Bellwood, 1988).

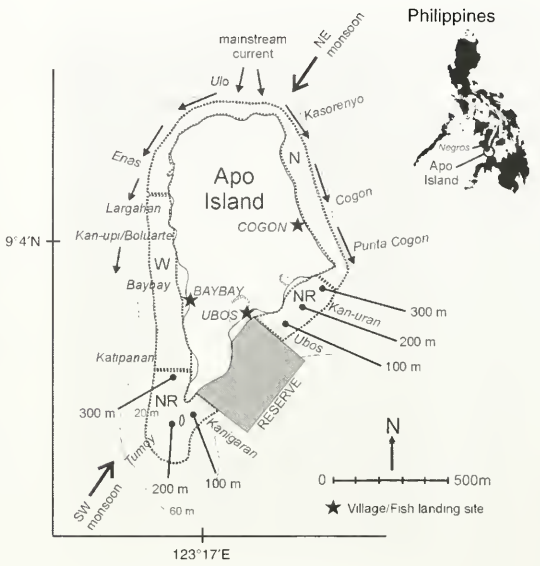

Figure 1

Apo Island, central Philippines, showing the no-take reserve (shaded). Names of fishing grounds around the island are italicized. Fishing grounds were grouped into "northern fishing grounds" (N), "western fishing grounds" (W), and "fishing grounds near Apo Reserve" (NR). The reef area of each of the fishing grounds is outlined (0–20 m isobath). Within the fishing grounds near Apo Reserve, the approximate positions of marker buoys used to indicate distance from either the northern or southern boundary of the reserve are shown. The major fish landing sites were at Baybay, Ubos, and Cogon villages (stars). Large arrows indicate the direction of the monsoons. Smaller arrows indicate direction of the mainstream current.

Data collection

The catches of fishermen residing at Apo Island were recorded daily from 22 July 2003 to 29 February 2004. Records were kept by three fish buyers, one buyer at each of the three major fish landing sites (the houses of the fish buyers) on the island, in Baybay, Ubos, and Cogon villages (Fig. 1). The fish buyers recorded the local names and weights of each species or family of fish that contributed to the catch sold by each fishermen. Catches were weighed on market scales accurate to 0.1 kg. The value of the catch sold by fishermen was estimated by multiplying the weight of each species by its average market price per kilogram in 2003, in Philippine Pesos (PHP). In addition, a resident research assistant (A. Candido) and one of the fish buyers (M. Aldeon) collected information from fishermen at each of the three villages through interviews every few days or weekly. The following information was gathered from fishermen:

fishing grounds visited, names and number of fishers, date and times when fishing started and finished, fishing gear used, and composition and weights of catches (verified from records of fish buyers). Interviewers were able to determine precisely where fishing was conducted because the names and locations of fishing grounds around Apo Island are common knowledge to local people (Fig. 1). However, if fishing was done near Apo Reserve (e.g., at Katipanan, Tumoy, Kanigaran, Ubos, and Kan-uran; Fig. 1), fishermen were also asked to estimate how far away they were from the boundaries of the reserve. Color-coded marker buoys, which fishermen could locate and identify easily while fishing, indicated approximate distances from reserve boundaries. These buoys were moored permanently at 100 m (blue), 200 m (red), and 300 m (yellow) from each of the northern and southern boundaries of Apo Reserve (Fig.1). The buoys were installed with the aid of a GPS receiver and fishermen were informed about them one week before the study started.

Data were collected from 80 full-time and part-time resident fishermen (Baybay–16, Ubos–47, Cogon–17). This group comprised 70–80% of all fishermen at Apo Island. The information in the present study probably reflects accurately the actual patterns of fishing effort and yield of the local market-oriented fishery. The majority of fishermen at Apo Island sell their catch to fish buyers at each of the three fish landing sites monitored (Maypa et al., 2002). The fish buyers usually purchased their fish from a group of "loyal" fishermen. Also, most fishermen live close to the houses of the fish buyers (landing sites). Thus, interviewers were able to collect data from fishermen regularly. Fishing effort and yield data were not adjusted to account for all resident fishermen (i.e., any fishermen not included in interviews).

However, data were not obtained from the following: 1) catch sold to part-time fish buyers on the island, 2) catch sold directly to the main island of Negros, 3) fishermen visiting from Negros, 4) catch sold dried, and 5) catch brought directly to homes for consumption. Items 1–4 are probably minor contributors to the total marketed yield. Maypa et al. (2002) surveyed the same fish landing sites monitored in the present study and estimated that only 10% of the total marketed yield (presumably from items 1–4) did not pass through the three major fish landing sites. On the other hand, yield from subsistence fishing (item 5) may be comparable in quantity to the marketed yield (White and Savina, 1987), but lower in monetary value. It is unlikely, however, that data on fishing effort collected in this study would differ much from data on subsistence fishing. It seemed common that fishermen went to sea to catch fish both to sell and keep for personal consumption.

Data analysis

Targeted species were classified into five groups according to Bellwood (1988): reef-associated species (Carangidae and Sphyraenidae), reef planktivores (Acanthuridae, Caesionidae, and Pomacentridae), reef species (mainly Lutjanidae, Lethrinidae, Scaridae, Serranidae, Kyphosidae, and octopus), open water species (Belonidae, Elopidae, and Scombridae), and off-reef species (Lutjanidae). Fishing grounds were classified into three groups: the northern fishing grounds (Enas, Ulo, Kasorenyo, Cogon, Punta Cogon), the western fishing grounds (Largahan, Kan-upi/Boluarte, Baybay, Katipanan), and the fishing grounds near Apo Reserve (Tumoy, Kanigaran, Ubos, Kan-uran) (Fig.1). Data were included in the third group if fishing was done ≤300 m from reserve boundaries. These three fishing grounds had roughly similar surface areas to the 20-m isobath (northern fishing grounds, 17.3 ha; western fishing grounds, 14.3 ha; fishing grounds near Apo Reserve, 18.9 ha). It was assumed that most fishing was done within or just outside the reef area enclosed by the 0- and 20-m isobaths (Fig. 1). In addition, data for the fishing grounds near Apo Reserve were classified into the following categories of distance from reserve boundaries: 0–100 m, 100–200 m, and 200–300 m.

Interviews allowed collection of fishing effort data even when fishermen returned from trips without catching anything (i.e., fishermen who used hook and line, gill nets, and spear guns). On average, about 20% of total fishing trips (or 23% of total fishing effort in person hours) returned with no catches. This figure varied considerably according to fishing gear (hook and line: 48%, gill net: 3%, spear gun: 7%) and months. However, fishing effort data for trips with zero catch were collected only beginning in September. Hence, the recorded fishing effort (in person hours) in July and August was adjusted by adding a correction factor in order to account for fishing trips with no catches. Correction factors were calculated from the equation

$$EC = \left[ER \times (EZ / ET)\right] / \left[1 - (EZ / ET)\right], \quad (1)$$

where EC and ER = the correction factor (expressed in person hours) and recorded monthly fishing effort, respectively, for July or August; and

EZ and ET = the total fishing effort with zero catch and the total fishing effort, respectively, in September.

Values for September were used because this month is within the same season as July and August (SW monsoon). Correction factors were calculated per gear (hook and line, gill net, and spear gun) and per group of fishing grounds. However, prior to adjustment, the recorded monthly fishing effort for July was multiplied by three to obtain an estimate for a 30-day period. The yield for July was also multiplied by three to obtain a 30-day yield estimate. Catch per unit of effort (CPUE, in kg/person per hour for each month was calculated by taking the average CPUE of all individual fishing trips made in a given month. Monthly CPUE was calculated per gear, per group of fishing grounds, and per distance from reserve boundaries (0–100, 100–200, and 200–300 m). July and August CPUE were adjusted

to account for fishing trips with zero catch, by adding correction factors (expressed in number of fishing trips) calculated by using Equation 1. Hence, correction factors were the number of fishing trips with zero CPUE. Income per unit of effort (IPUE) was used as an indicator of economic value among fishing grounds. This was calculated in the same manner as CPUE, expressed in PHP/person per hour. IPUE for July and August were adjusted in the same manner as CPUE.

ANOVA was used to determine how fishing effort for each of the three principal gear (hook and line, gill net, and spear gun [fish traps were rarely used]) varied according to seasons (SW monsoon and interim period vs. NE monsoon) and fishing grounds (northern, western, and near Apo Reserve). ANOVA was also used to determine how CPUE or IPUE varied according to fishing grounds and the three principal fishing gear and how CPUE varied according to distance from reserve boundaries (0–100, 100–200, 200–300, and >300 m) and the three principal fishing gears. Monthly estimates of each variate of interest were used as replicates in each ANOVA. Variates were transformed (log $[x+1]$ or square root $[x+1]$) to satisfy ANOVA assumptions. Tukey's test (Zar, 1999) was used in all *post hoc* analyses.

Two sets of indicators of relative economic value were used besides IPUE. The first was the frequency of capturing high-value species, and the frequency of landing a high yield of such species, expressed in number of fishing trips. This was summarized per species group and per fishing ground. High-value species were those with the highest, or the first and second highest, price per kg within species groups. Determination of a "high yield" within high-value species depended upon the average sizes of individuals within species groups, and whether species were usually landed as individuals or as groups. The following were considered high yield for high-value species: reef associated species (Carangidae, 3 spp.), ≥7.0 kg; reef planktivores (Caesionidae, 2 spp.), ≥3.0 kg; reef species (Serranidae, 3 spp., Lutjanidae, 7 spp., Lethrinidae, 2 spp.), ≥2.0 kg; open water species (Scombridae, 2 spp.), ≥7.0 kg; off-reef species (Lutjanidae, 1 sp.), ≥2.0 kg. The second indicator of economic value was the probability of capturing high-value species, and the probability of landing a high yield of such species, calculated on the basis of one fishing trip. This was calculated by dividing the frequencies (the first set of indicators) by the total number of fishing trips that used appropriate fishing gear to capture high-value species. Probabilities were calculated per species group and per fishing ground. Yield from traps were excluded in this analysis.

Results

Seasonal patterns of fishing effort and catch composition among fishing grounds

Hook-and-line fishing The majority of hook-and-line effort (73–98%) was made on the northern fishing grounds from July to December (Fig. 2A). However, during this period, hook-and-line fishing on the northern fishing grounds declined steadily (from 2302 to 50 person hours/month). It remained at low levels from January to February (35–173 person hours/month). Hook-and-line effort on the northern fishing grounds averaged 1015 ±342 (SE) person hours/month. The total hook-and-line yield from this area was 3549 kg (Table 1), dominated by reef-associated species (57%, mainly Carangidae) and reef planktivores (24%, mainly *Naso* spp.). Hook-and-line effort on the western fishing grounds was much lower, averaging 56 ±22 person hours/month (Fig. 2A). However, in January and February, hook-and-line effort on the western fishing grounds increased slightly (52–93 person hours/month). During this period, 38–62% of the total hook and line effort was made on the western fishing grounds, targeting an off-reef species (*Aphareus furca* (Lacepede) [Lutjanidae]). The total hook-and-line yield from the western fishing grounds was only 202 kg (Table 1), dominated by off-reef species (37%). Hook-and-line effort on the fishing grounds near Apo Reserve was the lowest among fishing grounds, averaging 33 ±9 person hours/month (Fig. 2A). It did not exhibit distinct seasonal patterns. The total hook-and-line yield near the reserve was only 166 kg (Table 1), dominated by reef species (38%, mainly octopus).

Hook-and-line effort (square root $[x+1]$ transformed) differed significantly between seasons (ANOVA, $F_{1,18}$= 13.14, P=0.002) and among fishing grounds (ANOVA, $F_{2,18}$= 35.08, P<0.001). The season by fishing ground interaction was significant (ANOVA, $F_{2,18}$=16.34, P<0.001). During the SW monsoon and interim period (July to October), hook-and-line effort on the northern fishing grounds was significantly higher than on the western fishing grounds (Tukey's test, $q_{3,18}$=12.45, P<0.001) and on the fishing grounds near Apo Reserve (Tukey's test, $q_{3,18}$=11.84, P<0.001). During the NE monsoon (November to February), hook-and-line effort did not differ significantly among fishing grounds. Hook- and-line effort on the northern fishing grounds was significantly higher during the SW monsoon and interim period (July to October) than during the NE monsoon (November to February) (Tukey's test, $q_{2,18}$=9.48, P<0.001). No significant differences in hook-and-line effort between seasons were found on the western fishing grounds and on the fishing grounds near Apo Reserve.

Gillnet fishing Gillnet fishing occurred mostly on the northern fishing grounds (194–466 person hours/month) from July to October (Fig. 2B). Gillnet effort on the northern fishing grounds averaged 268 ±44 person hours/month. The total gillnet yield from this area was 724 kg (Table 1), dominated by reef planktivores (76%, mainly Caesionidae). Beginning in November, gillnet effort shifted from the northern to the western fishing grounds. Gillnet effort on the western fishing grounds increased dramatically from zero in July, to 545 person hours/month in November (Fig. 2B). From November to February, the western fishing grounds accounted for 36–63% of the total gillnet effort. Gillnet effort on

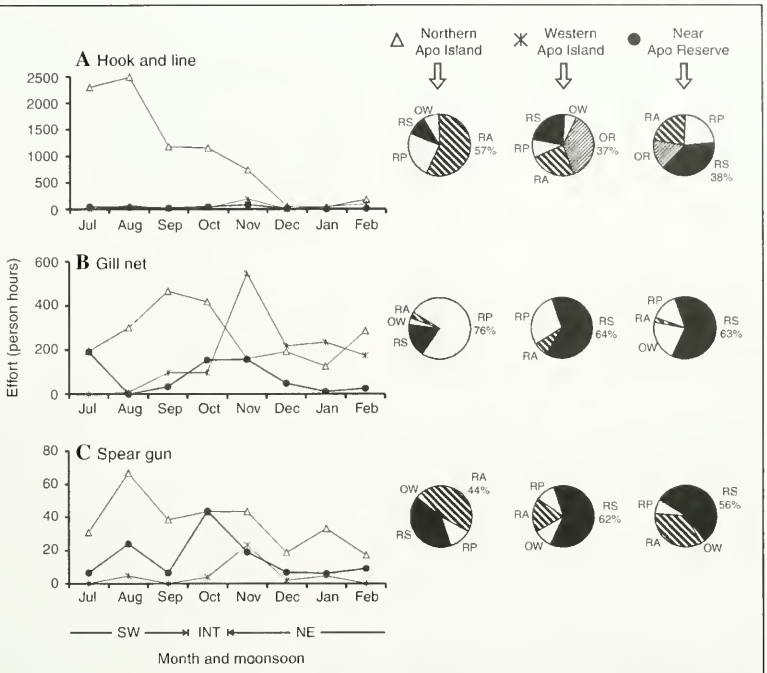

Figure 2

Seasonal trends in fishing effort (left-hand side) and composition of yield (right-hand side) for (**A**) hook-and-line, (**B**) gillnet, and (**C**) spear gun gear used at the three fishing grounds at Apo Island. Seasons: SW=southwest monsoon, INT=calm interim period, NE=northeast monsoon. Species groups: RA=reef associated species, RP=reef planktivores, RS=reef species, OW=open water species, OR=off-reef species. Percentages of dominant species groups are indicated. Legend for graphs at the left-hand side is at the upper right-hand side.

the western fishing grounds averaged 172 ±62 person hours/month. The total gillnet yield from this area was 493 kg (Table 1), dominated by reef species (64%, mainly Scaridae). Gillnet effort near Apo Reserve was much lower compared to other fishing grounds, averaging 78 ±27 person hours/month only. However, gillnet effort was relatively high near the reserve in July, October, and November (193, 155, and 157 person hours/month, respectively) (Fig. 2B). The total gillnet yield near the reserve was 318 kg (Table 1), dominated by reef species (63%, mainly Scaridae).

Gillnet effort did not differ significantly with seasons (ANOVA, $F_{1,18}$=0.18, P=0.68), but differed significantly among fishing grounds (ANOVA, $F_{2,18}$=6.72, P=0.007). The season by fishing ground interaction was significant (ANOVA, $F_{2,18}$=7.66, P=0.004). During the SW monsoon or interim period (July to October), gillnet effort on the northern fishing grounds was significantly higher than on the western fishing grounds (Tukey's test, $q_{3,18}$=5.68, P<0.005) and on the fishing grounds near Apo Reserve (Tukey's test, $q_{3,18}$=4.81, P<0.01) but did not differ between the latter two fishing grounds. During the NE monsoon (November to February), gillnet effort did not differ between the western and northern fishing grounds, but gillnet effort on the western fishing grounds was significantly higher than near Apo Reserve ($q_{3,18}$=4.47, P<0.025). Gillnet effort on the northern fishing grounds was higher during the SW monsoon and interim period than during the NE monsoon (Tukey's test, $q_{2,18}$=2.96, P=~0.05 [$q_{0.05,\ 2,18}$=2.97]). Conversely, gillnet effort on the western fishing grounds was significantly higher during the NE monsoon than during the SW monsoon and interim period (Tukey's test, $q_{2,18}$= 4.67, P<0.005). Gillnet effort near Apo Reserve did not differ significantly between seasons.

Spear gun fishing Spear fishing occurred mainly on the northern fishing grounds (Fig. 2C). However, spear

Table 1

Summary of recorded fishing effort, yield, and income of the fishery at Apo Island from 22 July 2003 to 29 February 2004. Contributions of the three fishing grounds (see Fig. 1) are shown. PHP = Philippine peso.

	Hook and line	Gill net	Spear gun	Fish trap	Overall
Total fishing effort (person hours)	8840	4141	452	129[1]	13,443[2]
Percent contribution					
Northern Apo Island	91.9	51.8	63.3	100	78.6
Western Apo Island	5.0	33.1	8.4	0	13.8
Near Apo Reserve	3.1	15.1	28.3	0	7.6
Total yield (kg)	3917	1535	406	32[3]	5890[3]
Percent contribution					
Northern Apo Island	90.6	47.2	66.2	100	77.7
Western Apo Island	5.2	32.1	4.8	0	12.1
Near Apo Reserve	4.2	20.7	29.0	0	10.2
Total income (PHP)	242,026	68,028	23,509	1371[3]	334,934[3]
Percent contribution					
Northern Apo Island	90.4	49.7	67.6	100	80.6
Western Apo Island	5.5	31.6	4.2	0	10.7
Near Apo Reserve	4.1	18.7	28.2	0	8.7

[1] Fishing effort in trap days = number of traps × number of days traps were left on the reef.

[2] Excludes fish trap effort.

[3] Trap yield in July not adjusted to 30-day period.

gun effort in this area declined from August to February (67 to 17 person hours/month, respectively). Spear gun effort on the northern fishing grounds averaged 36 ±6 person hours/month. The total spear gun yield from the northern fishing grounds was 269 kg (Table 1), dominated by reef-associated species (44%, Carangidae). Spear gun effort on the western fishing grounds was much lower, averaging only 5 ±3 person hours/month. It was highest in November (23 person hours/month) (Fig. 2C). The total spear gun yield from the western fishing grounds was only 19 kg (Table 1), dominated by reef species (62%, mainly Scaridae and octopus). Spear gun effort near the boundary of Apo Reserve was also rather low but was higher on average than on the western fishing grounds (mean 15 ±5 person hours/month). It peaked in October (44 person hours/month) (Fig. 2C). The total recorded spear gun yield near the reserve was 118 kg (Table 1), dominated by reef species (56%, mainly Scaridae and octopus).

Spear gun effort did not differ significantly between seasons (ANOVA, $F_{1,18}$=2.12, P=0.16) but differed significantly among fishing grounds (ANOVA, $F_{2,18}$=14.26, P<0.001). The season by fishing ground interaction was not significant (ANOVA, $F_{2,18}$=1.77, P=0.20). Spear gun effort on the northern fishing grounds was significantly higher than on the western fishing grounds (Tukey's test, $q_{3,18}$=7.41, P< 0.001) and the fishing grounds near Apo Reserve (Tukey's test, $q_{3,18}$=4.96, P<0.01). Spear gun effort, however, did not differ significantly between the fishing grounds near Apo Reserve and the western fishing grounds of Apo Island.

Trap fishing Bamboo fish traps were used on the northern fishing grounds only, and only in July (SW monsoon). The total trap effort was 126 trap days (4 fish traps set for 14 days, 7 for 10 days) with a total yield of 32 kg (Table 1). The yield was dominated by reef planktivores (85% Acanthuridae and Caesionidae).

Contributions of fishing gears and fishing grounds to overall fishing effort, yield, and income

Among the three principal fishing gear, most fishing effort was spent with hook and line, followed by gill nets, then with spear guns (Table 1). Hook-and-line fishing, therefore, contributed the greatest yield and highest income, accounting for 66% of the total yield and 72% of the total income recorded. Bamboo fish traps contributed the least yield and income (Table 1). All types of fishing occurred mainly on the northern fishing grounds. The northern fishing grounds accounted for 92%, 52%, 63%, and 100% of the total effort for hook-and-line gear, gill nets, spear guns, and fish traps, respectively. Accordingly, the northern fishing grounds accounted for the vast majority of total yield and total income for all types of fishing gears (Table 1).

On the other hand, fishing effort was often lowest on the fishing grounds near Apo Reserve (Table 1). The fishing grounds near the reserve accounted for only 3% and 15% of the total effort spent on hook-and-line and gillnet fishing, respectively. These fishing grounds contributed only 4% to the total yield and total income from hook and line fishing, and only 21% to the total

yield and 19% to the total income from gillnet fishing. Only 28% of the total spear gun effort was made near Apo Reserve. However, the overall spear gun effort near the reserve was about three times higher than that on the western fishing grounds. The fishing grounds near the reserve contributed about six times the yield and seven times the income of spear fishing on the western fishing grounds (Table 1).

Among species groups, the highest yield recorded was for reef-associated species, followed by reef planktivores, and then reef species (Table 2). Open water and off-reef species were minor contributors to overall yield. Reef-associated species together with reef planktivores accounted for 69% of the overall yield. The northern fishing grounds contributed ≥80% of the total yield of reef-associated species, reef planktivores, and open water species (Table 2). Much of the total yield of reef species (47%) was also taken from the northern fishing grounds. The western fishing grounds contributed 68% of the total yield of off-reef species but accounted for little of the yield for other species groups (Table 2). The fishing grounds near Apo Reserve often accounted for the smallest contribution to yield for all species groups. However, about a quarter of the total recorded yield of reef species were taken near the reserve.

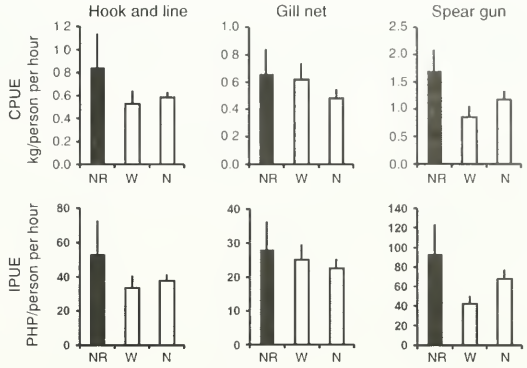

Figure 3

Mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for hook-and-line, gillnet and spear at the three fishing grounds at Apo Island. NR=near Apo Reserve, W=western Apo Island, N=northern Apo Island (see Fig. 1). Error bars are 1 standard error. PHP=Philippine peso.

Table 2

Composition of total recorded yield of the fishery at Apo Island from 22 July 2003 to 29 February 2004. Contributions of the three fishing grounds (see Fig. 1) are shown. Species groups: RA=reef-associated species, RP=reef planktivores, RS=reef species, OW=open water species, OR=off-reef species. Yield in July adjusted to 30-day period for each species group. Table excludes 16 kg of unidentifiable catch.

	RA	RP	RS	OW	OR
Total yield (kg)	2333	1772	1305	418	111
Percent contribution					
Northern Apo Island	92.4	85.6	46.7	80.0	7.9
Western Apo Island	3.9	9.1	28.4	3.6	67.5
Near Apo Reserve	3.7	5.2	24.9	16.4	24.6

Spatial patterns of CPUE and IPUE among fishing grounds

Mean hook-and-line, gillnet, and spear gun CPUE were highest in the fishing grounds near Apo Reserve (Fig. 3). CPUE near the reserve was higher than on the northern fishing grounds by a factor of 1.5, 1.4 and 1.4 for hook-and-line, gillnet, and spear fishing, respectively. CPUE near the reserve was higher than on the western fishing grounds by a factor of 1.6, 1.1 and 2.0 for hook-and-line, gillnet, and spear fishing, respectively. However, ANOVA indicated that CPUE (log [x+1] transformed) did not differ significantly among the three groups of fishing grounds ($F_{2,57}$=1.87, P=0.16), but differed significantly among fishing gear ($F_{2,57}$=9.26, P<0.001).

The trends in mean IPUE reflected closely those of CPUE (Fig. 3). Mean IPUE near the reserve was higher than on the northern fishing grounds by a factor of 1.4, 1.2, and 1.4 for hook-and-line, gillnet and spear fishing, respectively. It was higher than on the western fishing grounds by a factor of 1.6, 1.1 and 2.2 for hook-and-line, gillnet, and spear fishing, respectively. However, ANOVA indicated that IPUE (log [x+1] transformed) did not differ significantly among the three groups of fishing grounds ($F_{2,57}$=0.49, P=0.62), but differed significantly among fishing gear ($F_{2,57}$=6.77, P=0.002).

Monthly mean hook-and-line, gillnet, and spear gun CPUE and IPUE near Apo Reserve were more variable than in the other fishing grounds (Fig. 4, A–C). For example, the monthly hook-and-line CPUE near Apo Reserve changed from >1.5 to <1.0 to >2.0 and to <1.5 kg/person per hour from July to October. However, from November to February, it remained at <0.5 kg/person per hour, but was zero in January (Fig. 4A). Monthly hook-and-line IPUE near Apo Reserve varied accordingly. It changed from >100 to <50 to >150 and to <100 PHP/person per hour from July to October, but was less than 30 PHP/person per hour from November to February and was zero in January. In contrast, the monthly

hook- and-line CPUE and IPUE on the northern and western fishing grounds of Apo Island exhibited little variability (Fig. 4A). For most of the period between July and February, the monthly hook-and-line CPUE on the northern fishing grounds remained between 0.5 to 0.8 kg/person per hour, whereas IPUE remained between 30 to 50 PHP/person per hour. Monthly CPUE for the western fishing grounds remained mostly between 0.2 to 1.0 kg/person per hour, whereas monthly IPUE remained mostly between 15 to 60 PHP/person per hour.

Fishing grounds near Apo Reserve often had the lowest minimum monthly CPUE and IPUE for all fishing gears, except for spear gun, which had the lowest minimum monthly CPUE and IPUE on the western fishing grounds (Table 3). However, fishing grounds near Apo Reserve always had the highest maximum monthly CPUE and IPUE for all fishing gears (Table 3, Fig. 5). Maximum monthly CPUE near the reserve was higher by a factor of 1.2 to 3.0, depending on the fishing gear and fishing ground (Fig. 5). Maximum monthly IPUE near the reserve was higher by a factor of 1.6 to 4.3, depending on the fishing gear and fishing ground. On the other hand, the highest minimum monthly CPUE and IPUE for all fishing gears were most often found only on the northern fishing grounds of Apo Island (Table 3).

Table 3

Range of monthly mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for hook-and-line, gillnet, and spear gun gear at the fishing grounds at Apo Island (see Fig. 1). Lowest minimum and highest maximum average values are marked by the symbol †. Highest minimum values are marked by ‡. PHP = Philippine peso.

	Hook and line	Gill net	Spear gun
CPUE (kg/person per hour)			
Northern Apo Island	0.3‡–0.8	0.2‡–0.7	0.7‡–2.0
Western Apo Island	0.1–1.0	0.2‡–1.3	0.2‡–1.5
Near Apo Reserve	0.0‡–2.4†	0.1†–1.6†	0.5–3.9†
IPUE (PHP/person per hour)			
Northern Apo Island	18.4‡–49.00	9.6‡–31.30	40.30‡–117.60
Western Apo Island	6.20–58.40	8.20–46.40	11.90‡–57.80
Near Apo Reserve	0†–154.90†	7.80‡–73.70†	30.50–249.90†

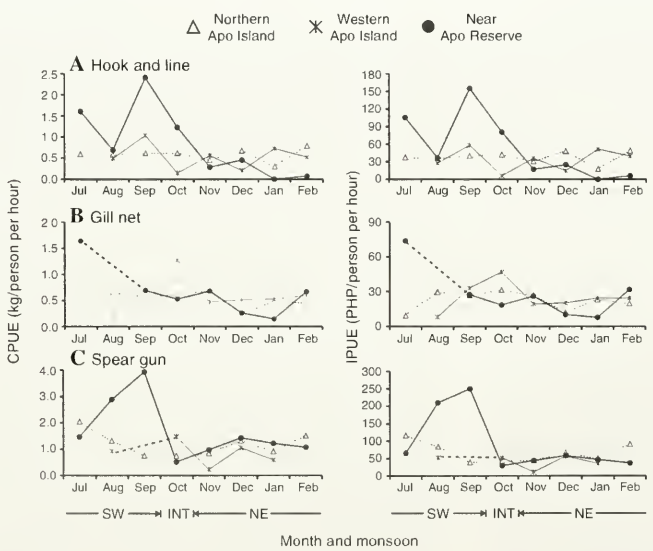

Figure 4

Monthly mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for (**A**) hook-and-line, (**B**) gill-net, and (**C**) spear at the three fishing grounds at Apo Island. Seasons: SW=southwest monsoon, INT=calm interim period, NE=northeast monsoon. PHP=Philippine peso.

Spatial patterns of high-value catches among fishing grounds

Capturing high-value species and landing a high yield of such species were often more frequent on the northern fishing grounds (Table 4). For example, 133 captures of high-value reef-associated species (Carangidae—*Caranx ignobilis* (Forsskål), *Caranx melampygus* (Cuvier), and *Carangoides* sp.) were made on the northern fishing grounds. In 46 of these captures, the yield was ≥7.0 kg or 525 PHP. Six of the fishes cap-

Table 4

Frequency and probability of capturing or landing a high yield of high-value species within each species group for each of the three fishing grounds at Apo Island (see Fig. 1). Upper values: frequency (number of fishing trips) and probability (in parentheses) of capturing high-value species. Lower values: frequency (number of fishing trips) and probability (in parentheses) of landing a high yield of high-value species. Highest frequencies are marked with the symbol †. Highest probabilities are marked with the symbol ‡. Price per kg and prices of what were considered "high yield" are given in Philippine pesos (PHP).

Species groups, families	Northern Apo Island	Western Apo Island	Near Apo Reserve
Reef-associated species (Carangidae)			
75 PHP/kg	133† (0.07)‡	9 (0.03)	8 (0.05)
≥7.0 kg or PHP 525	46† (0.03)‡	1 (0.004)	4 (0.02)
Reef planktivores (Caesionidae)			
55 PHP/kg	123† (0.07)‡	17 (0.06)	9 (0.05)
≥3.0 kg or PHP 165	36† (0.03)‡	4 (0.02)	0 (0)
Reef species (Serranidae, Lutjanidae, Lethrinidae)			
70–75 PHP/kg	57† (0.03)	15 (0.06)	12 (0.07)‡
≥2.0 kg or PHP 150	31† (0.02)	10 (0.04)	9 (0.05)‡
Open water species (Scombridae)			
75–90 PHP/kg	5† (0.003)	1 (0.01)‡	0 (0)
≥7.0 kg or PHP 525	3† (0.002)‡	0 (0)	0 (0)
Off-reef species (Lutjanidae)			
75 PHP/kg	4 (0.003)	29† (0.23)‡	3 (0.04)
≥2.0 kg or PHP 150	2 (0.001)	13† (0.10)‡	2 (0.03)

tured weighed ≥15 kg (equivalent to a value of ≥1125 PHP). The largest was a 31.9-kg *C. ignobilis* valued at 2393 PHP, which was also the biggest fish caught during our study. In contrast, only eight captures of high-value reef-associated species were made near Apo Reserve. In only four of these captures were the yields ≥7.0 kg or 525 PHP. Only one of the fishes captured near the reserve weighed >15 kg. This was a 20.2-kg *C. ignobilis* valued at 1515 PHP.

Capturing high-value species and landing a high yield of such species often had the greatest probability of occurring on the northern fishing grounds (Table 4). For example, the probability of capturing high-value reef-associated species from the northern fishing grounds was 0.07. Landing a high yield of such species from this area had a probability of 0.03. In contrast, the probability of capturing high-value reef-associated species near Apo Reserve was 0.05. Landing a high yield of such species near the reserve had a probability of 0.02. However, the probability of capturing high-value reef species (Serranidae—*Cephalopholis*, *Epinephelus*, *Variola* spp.; Lutjanidae—*Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus* spp.; and Lethrinidae—*Lethrinus* spp.) was greatest near Apo Reserve (Table 4). The probability of landing a high yield of such species (≥2.0 kg or 150 PHP) was also greatest near the reserve, despite the higher frequency of capturing high-value reef species, or landing a high yield of such species, on the northern fishing grounds than near Apo Reserve (Table 4).

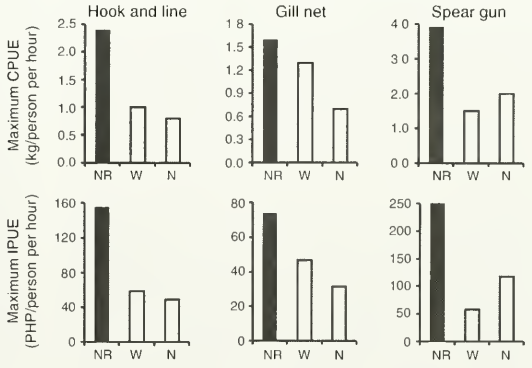

Figure 5

Maximum monthly mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for hook-and-line, gill-net, and spear gun gear used at the three fishing grounds at Apo Island. NR=near Apo Reserve, W=western Apo Island, N=northern Apo Island (see Fig. 1). Error bars are 1 standard error. PHP=Philippine peso.

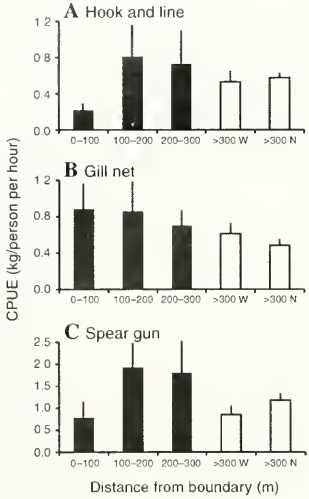

Figure 6

Mean catch per unit of effort (CPUE) for (**A**) hook-and-line, (**B**) gillnet, and (**C**) spear gun gear deployed at three distances from the boundary of Apo Reserve (0–100, 100–200, 200–300 m [shaded columns]; refer to Fig. 1) and at two areas far (>300 m) from reserve boundaries (W=western Apo Island fishing ground, N=northern Apo Island fishing ground [open columns]; refer to Fig. 1). Error bars are 1 standard error.

Spatial patterns of CPUE near reserve boundaries

Spatial patterns of CPUE away from reserve boundaries differed for hook-and-line, gillnet, and spear gun gear (Fig. 6). Gillnet CPUE exhibited a pattern of decrease from 0–100 to 200–300 m from the reserve boundaries (from 0.88 to 0.70 kg/person per hour; Fig. 6B). Gillnet CPUE further decreased >300 m from reserve boundaries (western and northern fishing grounds). In contrast, hook-and-line and spear gun CPUE was lowest near (0–100 m) reserve boundaries, but much higher at distances of 100–300 m from the boundaries (Fig. 6, A and C). Hook-and-line and spear gun CPUEs at 100–300 m from reserve boundaries were higher than farther away (>300 m) from the boundaries (western and northern fishing grounds). However, hook-and-line and spear gun CPUEs were highest at 100–200 m from reserve boundaries (Fig. 6, A and C). An ANOVA with data for 0–300 m indicated only that CPUE did not differ significantly with distance from reserve boundaries ($F_{2,39}$=0.73, P=0.49) or with fishing gear ($F_{2,39}$=2.52, P=0.09). However, an ANOVA with data for 0–300 and >300 m indicated that CPUE (log [x+1] transformed) did not differ significantly with distance from reserve boundaries ($F_{4,76}$=1.19, P=0.32) but differed significantly among fishing gear ($F_{2,76}$=7.28, P=0.001).

Table 5

Frequency of fishing trips for each of the three distances from the boundaries of Apo Reserve (see Fig. 1), for each of hook and line, gill net, and spear gun. Fishing trips were made between 22 July 2003 and 29 February 2004.

	Number of times fished		
	Hook and line	Gill net	Spear gun
Distance from reserve boundaries			
0–100 m	2	3	4
100–200 m	43	24	33
200–300 m	25	28	7

Contrasting patterns were also found in fishing effort (frequency of fishing trips) at different distances from the boundaries of Apo Reserve (Table 5). Hook-and-line and spear fishing occurred most frequently at intermediate distances from reserve boundaries, but gillnet fishing occurred most frequently at the farthest distances. However, all types of fishing occurred very infrequently within 100 m of reserve boundaries (Table 5).

Discussion

Results indicate that the maximum possible contribution of spillover from the no-take reserve to the overall yield and income of the fishery at Apo Island is small. If one assumes that the spillover of coral reef fishes is most likely to operate on spatial scales of hundreds of meters (Russ, 2002), and, thus, would be unlikely to affect fishery yields on the western and northern fishing grounds, the maximum possible contribution would be 10% of the total fishery yield, but the real value is probably much less than this. We assumed that the eight months sampled in 2003–2004 are representative of the general spatial pattern of fishing at Apo Island. Furthermore, we assumed that the spatial pattern of fishing during the four months not sampled (March to June) remains consistent with the general pattern of fishing. It can be estimated from the present study that the total fishery yield at Apo Island in 2003–2004, excluding the yield consumed locally, was around 10.4 tons/km^2 per year (to the 60-m isobath). Thus, spillover from Apo Reserve would have contributed very much less than 1.0 ton/km^2 per year in 2003–2004.

Fishing effort was often lowest on the fishing grounds near the reserve. The fishery at Apo Island is primarily hook and line, targeting reef-associated species (Carangidae), and to a lesser extent reef planktivores (*Naso*

spp.) (Alcala and Luchavez, 1981; White and Savina, 1987; Bellwood, 1988; Maypa et al., 2002; present study). Ninety-two percent of total hook-and-line effort was made on the northern fishing grounds of the island. Gill nets, spear guns, and fish traps were not used as much as hook-and-line; however, fishing with these gear was also carried out mostly on the northern fishing grounds, contributing to a yield of reef-associated species and reef planktivores. Fishing near Apo Reserve contributed mainly to catch of reef species (Scaridae and octopus), which are a less important species group for the local fishery. The fishery depended heavily on access to the northern fishing grounds during the SW monsoon and calm interim period (Bellwood, 1988; present study). Results clearly showed that fishing effort on the northern fishing grounds was considerably lower during the NE monsoon, especially for hook-and-line gear and gill nets. However, fishing effort did not shift to the fishing grounds near Apo Reserve during the NE monsoon. Gillnet fishing seemed to transfer instead to the western fishing grounds, targeting reef species (Scaridae). To a much lesser degree, hook-and-line fishing also transferred to the western fishing grounds, targeting high-value off-reef species (*Aphareus furca* [Lutjanidae]). The northern fishing grounds alone accounted for 78% of overall yield and 81% of overall income recorded in our study (Table 1). In contrast, fishing grounds near Apo Reserve accounted for only 10% of overall yield and 9% of overall income (Table 1). However, it is highly unlikely that spillover from Apo Reserve supplied the entire yield taken from fishing grounds near the reserve. That is, the yield near the reserve was probably not composed totally of migrants from the reserve. Therefore, the actual spillover contribution of Apo Reserve would be much less than 10% to the overall yield and income generated by the fishery.

However, CPUE of fishermen was highest on the fishing grounds near Apo Reserve. This pattern may have resulted from 1) spillover from the reserve or 2) lower fishing intensity near the reserve, resulting in higher abundance of fish and, thus, higher CPUE. There is far more empirical evidence supporting the spillover hypothesis than the lower fishing intensity hypothesis. Considerable evidence exists that some supplement for the fishery near the reserve has developed over time. Firstly, monitoring of Apo Reserve since 1983 has shown that fish populations inside the reserve have increased in abundance, some having tripled in density or biomass over the last two decades (Russ and Alcala, 1996, 1998, 2003; Russ et al., 2003, 2004; Alcala et al., 2005). Secondly, long-term monitoring indicates that the reserve began to export adult fish to a site open to fishing after ~8 years of reserve protection (Russ and Alcala, 1996; Russ et al., 2003, 2004). Thirdly, catch rates of some species (Acanthuridae) were found to be higher near the reserve than elsewhere around Apo Island after two decades of reserve protection (Russ et al., 2003, 2004). Fourthly, recent studies indicate that patterns of decreasing abundance of some targeted species are present across the northern boundary of the reserve (Abesamis et al., 2005). Lastly, a recent study indicates that density-dependence may be driving net emigration of adult fish (*Naso vlamingii* (Valenciennes)) from the reserve (Abesamis and Russ, 2005). On the other hand, no direct evidence is available to show that fishing effort near Apo Reserve has remained low over the last two decades. However, the fishing grounds near the reserve may be partially exposed to the SW and NE monsoons (Alcala and Luchavez, 1981). During the SW monsoon, the fishing grounds adjacent to the southern end of the reserve may become rough, but those adjacent to the northern end are usually calm (Fig. 1). The pattern is reversed during the NE monsoon. Thus, fishing effort near the reserve may be reduced for nine months of the year (June to September, November to March) because only the area close to one side of the reserve may be fished, depending on the monsoon. The role of the monsoons in limiting fishing effort near the reserve cannot be ruled out entirely.

If spillover has increased CPUE near the reserve, as long-term evidence seems to indicate, then why have local fishermen not responded noticeably to the improvement in catch rates? Weather may be important in limiting fishing effort near the reserve, but it cannot explain the low fishing intensity in this area during the calm interim months. Results show that hook-and-line and gillnet effort on the fishing grounds near the reserve in October were still considerably lower than on the northern fishing grounds (Fig. 2, A and B). Anecdotal information also indicates that most fishermen still prefer to fish the northern fishing grounds even during April and May (Pascobello[2]). This information is consistent with the findings of previous studies (White and Savina, 1987; Bellwood, 1988; Maypa et al., 2002), which indicate that the general pattern of fishing effort at Apo Island has not changed much since creation of the reserve in 1982. Furthermore, a reasonable amount of fishing area (8–11 ha) near the reserve is still available to fishermen during either monsoon. Given the higher catch rates, fishermen could still concentrate effort near the reserve, one side of the reserve at a time, depending on the monsoon. Higher costs (time and energy spent to paddle a small boat [*banca*]) are certainly not preventing fishermen from fishing adjacent to the reserve. The majority of fishermen (80%) reside near the reserve, in Baybay and Ubos villages (Fig. 1) and therefore for most fishermen the costs of fishing the northern side of Apo Island may actually be higher. It is also unlikely that fishermen are not aware of higher catch rates near the reserve. Fishermen can probably obtain good information about catch rates from the experiences of fellow fishermen, or from word-of-mouth, because the community is relatively small and tightly knit. Many fishermen are members of the same family (including cousins and uncles) or are friends with each other. Income rates *per se* can also be ruled out as an

[2] Pascobello, M. 2002. Personal commun. Apo Island resident and village chairman. Apo Island, Dauin Municipality, Negros Oriental, Philippines, 6217.

important influence on the spatial pattern of effort because results indicated that IPUE for all gears was also highest on the fishing grounds near the reserve. However, one cannot discount that the northern side of Apo Island may be regarded by the local community as their main traditional fishing ground. This area has probably been fished for decades, providing the income for families generation after generation.

Other characteristics of the CPUE and IPUE data may also provide a partial explanation. CPUE and IPUE were more variable on the fishing grounds near Apo Reserve (Fig. 4). In fact, the fishing grounds near the reserve often had both the highest and lowest CPUE and IPUE per month for all types of fishing gears (Table 3, Fig. 5). The only exception was for spear gun, which had the lowest CPUE and IPUE on the western fishing grounds (Table 3). These findings may indicate that near the reserve, fishermen could obtain very high average monthly catch rates and income rates. However, they may also indicate that near the reserve, fishermen (using hooks and lines and gill nets) could obtain very low average monthly catch rates and income rates. Monthly CPUE and IPUE were least variable on the northern fishing grounds (Fig. 4). In addition, the highest minimum average monthly CPUE and IPUE were always found in this area (Table 3). Therefore, a plausible explanation for the spatial pattern of fishing effort at the island scale is that fishermen probably tend to avoid fishing near Apo Reserve in order to make their monthly incomes more stable and avoid occasional very low catch rates. Fishermen may prefer the northern fishing grounds even if catch rates in this area are not as high as near the reserve because they are assured of obtaining higher minimum yields and a more stable income. This strategy may be a form of financial "risk aversion" (Hilborn and Walters, 1992). It is further postulated that such a risk aversion strategy could explain why total spear gun effort was higher on the fishing grounds near Apo Reserve than on the western fishing grounds (Tables 1 and 3). Also, a risk aversion strategy may partly explain why fishing with gill nets and hook and line transferred to the western fishing grounds instead of near the reserve during the NE monsoon (Fig. 2B, Table 3).

Other factors may also influence the decision by fishermen to concentrate effort on the northern side of Apo Island. For example, the largest and most valuable fish recorded in this study, a 31.9-kg *Caranx ignobilis* worth almost PHP 2400, was captured from the northern fishing grounds. A high-priced catch such as this one may have a tremendous psychological impact on local fishermen. Anecdotal information seems to indicate that the income from such a yield may be enough to provide for 80% of the daily expenses of one family for one month at Apo Island (Pascobello-Rhodes[3]). In comparison, the largest and most valuable fish caught near Apo Reserve, also *C. ignobilis*, was only two-thirds the weight (20.2 kg) and value (PHP 1515) of the largest fish caught from the northern fishing grounds. This fish was the only one caught near the reserve with a value greater than PHP 1000. Local fishermen probably consider fish of this size more common on the northern fishing grounds. During this study, five individuals of *C. ignobilis* (range: 15.0–19.0 kg) that were captured from the northern fishing grounds had weights similar to the largest fish caught near the reserve. Therefore, the biggest psychological impact on fishermen may not be due to spillover from the reserve.

A perception by local fishermen that the northern fishing grounds are productive areas for high-value species may not only have a psychological basis. Results indicate that the probability of capturing high-value reef-associated species (Carangidae) and the probability of landing a high yield of such species were highest on the northern fishing grounds (Table 4). The same was true for high-value reef planktivores (Caesionidae) (Table 4). The probability of landing a high yield of high-value open water species (Scombridae) was also greatest on the northern fishing grounds (Table 4). Assuming that fishermen prefer to target high-value species, these findings indicate that fishermen have better chances of making higher incomes from the northern fishing grounds than from other areas. The better prospect of making a higher income probably influences the decision by fishermen to concentrate effort on the northern side of Apo Island whenever it is accessible. Similarly, some fishermen probably shift to the western fishing grounds during the NE monsoon (the "off-season") because of better chances of gaining higher incomes by targeting high-value off-reef species (*A. furca* [Lutjanidae]) (Table 4).

However, the results indicated that the probability of capturing high-value reef species (Serranidae, Lutjanidae, and Lethrinidae), or landing a high yield of such species, was greatest on the fishing grounds near Apo Reserve (Table 4). Fishing intensity for high-value reef species, on the other hand, appears to be greatest on the northern fishing grounds, because capturing or landing a high yield of high-value reef species was most frequent there (Table 4). Thus, it seemed that most fishermen avoided fishing for high-value reef species near Apo Reserve despite better chances of making high incomes from high-value reef species. One plausible explanation for avoiding the fishing grounds hear the reserve is that fishermen would still prefer to fish the northern fishing grounds because they can target the high-value species that come in larger sizes (Carangidae and Scombridae) or greater numbers (Caesionidae) and at the same time occasionally capture high-value reef-species. The high-value reef species (Serranidae, Lutjanidae, Lethrinidae) are unsatisfactory alternatives for fishermen because they come in smaller sizes (compared to Carangidae and Scombridae) or in smaller numbers (compared to Caesionidae), and therefore would fetch a lower price.

[3] Pascobello-Rhodes, L. 2003. Personal commun. Apo Island resident. Apo Island, Dauin Municipality, Negros Oriental, Philippines, 6217.

On the other hand, the highest maximum monthly CPUE and IPUE were invariably found near Apo Reserve (Fig. 5, Table 3). This result is consistent with the occasional spillover of bigger fish from the reserve. Such an effect may have a positive influence on the attitudes of fishermen toward reserves (Russ and Alcala, 1996). However, in the case of the artisanal fishery at Apo Island, any psychological impact of large catches near the reserve on fishermen is probably attenuated by the importance of the northern fishing grounds. In other fisheries, however, occasional spillover of large adults may be important. Recreational "trophy" fisheries, for example, may benefit directly from such an effect of no-take reserves (Bohnsack, 1998; Johnson et al., 1999; Roberts et al., 2001). In New Zealand, Kelly et al. (2002) showed that lobster catch rates (kg/trap haul) were similar close to and far from Leigh Marine Reserve, although catches around the reserve consisted of fewer individuals. The lobsters caught near the reserve were bigger. Furthermore, the amount of money made per trap haul close to the reserve was similar to sites far from the reserve.

The findings at the scale of a few hundred meters from the boundary of the reserve provide little evidence to indicate that spillover from Apo Reserve is present. In fact, the most informative result at this spatial scale was that fishermen seemed to avoid fishing very close to the reserve (i.e., within 100 m from the boundaries) (Table 5). Furthermore, catch rates seemed to be lowest closest to reserve boundaries for hook-and-line and spear fishing (Fig. 6, A and C). However, gillnet fishing seemed to have a pattern of decreasing catch rate away from reserve boundaries (Fig. 6B). Gear selectivity interacting with the spatial distribution of target species may explain the differences in spatial patterns of CPUE among the three gears. Gillnet fishing is probably less selective than hook-and-line and spear fishing.

The pattern of fishing effort found very near to the reserve can be interpreted in two ways. Firstly, local fishermen may be well aware of the distribution of catch rates near Apo Reserve, and they adjust their fishing effort accordingly. This interpretation is supported to some degree by the correspondence between the pattern of CPUE and the pattern of fishing effort for hook-and-line and spear gun gear. Both CPUE and fishing effort for these gear were highest at intermediate distances (100–200 m), but lower at the closest (0–100 m) and farthest distances (200–300 m) from the reserve (Fig. 6, A and C, Table 5). Fishermen may know from experience that hook-and-line and spear gun catch rates are low nearest the reserve (0–100 m), hence they tend to avoid fishing in this area. Experimental fishing with hooks and line, but specifically targeting *N. vlamingii*, supports the contention that hook-and-line CPUE is low very close to the boundary of Apo Reserve (Abesamis and Russ, 2005). Hook-and-line CPUE for *N. vlamingii* was higher at intermediate distances (150–200 m) than at the closest (50–100 m) and farthest (250–300 m) distances from the reserve (Abesamis and Russ, 2005). Although movement of fish from Apo Reserve to sites at intermediate distances (100–200 m) from the reserve has never been demonstrated directly, research in the last two decades has shown that fish populations (Acanthuridae, Carangidae, Serranidae, Lutjanidae, and Lethrinidae) have increased outside but close to the southern boundary of the reserve (about 200–250 m from that boundary) after about eight years of reserve protection (Russ and Alcala, 1996; Russ et al. 2003, 2004). This increase in populations may indicate that the present spatial distribution of hook-and-line and spear gun effort at the local scale may reflect the response of a small number of fishermen to spillover from the reserve.

Secondly, local fishermen may avoid fishing very close to the boundaries of Apo Reserve in order to prevent being accused of poaching inside the reserve. The inconsistent result of a higher catch rate but lower fishing effort nearest the reserve for gillnet fishing supports this idea (Fig. 6B, Table 5). Furthermore, there may be tremendous motivation for resident fishermen not to be implicated in poaching inside the reserve. The ultimate reason for this probably lies in the smallness of the community at Apo Island. Almost everyone has known each other for most of their lives. The no-take reserve was established by the community for their own benefit (Russ and Alcala, 1999). It has been guarded and maintained by community members, many of them fishermen themselves, for most of the two decades of its existence (Russ and Alcala, 1999). It has an important role in tourism on the island, from which the local community has benefited considerably in many ways (Alcala, 1998; Russ and Alcala, 1999). It is the principal factor that has made Apo Island a nationally and internationally recognised model for successful, community-based resource management (Alcala, 1998; Russ and Alcala 1999). Many residents are probably aware of most, if not all, of these achievements. For these reasons, it is clearly against the best interests of a resident fisherman, and his family, to be labeled by fellow community members as a threat to the security of their reserve.

In conclusion, this study has shown that spillover yield from the no-take reserve at Apo Island probably contributes much less than 10% of the overall yield to the local fishery. Fishing effort was often lowest near the reserve, despite higher catch rates there. The finding of low fishing intensity near reserve boundaries despite indications of spillover contrasts with most empirical evidence collected so far (e.g., Gell and Roberts, 2003) and recent theoretical studies (e.g., Salomon et al., 2002) indicate that spillover will increase fishing effort near reserve boundaries. Fishing effort adjacent to the reserve appears to be limited by 1) weather determined by the monsoons, 2) the traditional importance of the northern fishing grounds, 3) high variability of catch rates and income rates, 4) lower value of target species found near the reserve, and 5) social pressures related to the history of community management of the reserve. However, the present study has no information on how fishing effort, yield, and catch rates near the reserve have changed over the past 20 years since

reserve establishment. Despite the Apo Island fishery being one of the best studied coral reef fisheries in the world (Alcala and Luchavez, 1981; White and Savina, 1987; Bellwood, 1988; Maypa et al., 2002; Russ et al, 2004; Alcala et al., 2005), the present study is the first to quantify detailed spatial variations in fishing effort, catch, and CPUE at Apo Island. Furthermore, it is not clear if spillover yield to the local fishery has reached its full potential or not. Long-term fishery monitoring is required to answer these questions. Although the reserve probably provides limited direct benefits to the local fishery through spillover, its indirect benefits to the community at Apo Island are considerable. The reserve became the foundation for a program of fishery conservation for the whole island, which eliminated unsustainable fishing practices such as dynamite fishing and muro-ami drive-net fishing. It played a critical role in enhancing tourism activities on the island, which had a tremendous positive effect on the standard of living of the local community (Russ and Alcala, 1999; White et al., 2002). These indirect effects of reserve establishment are arguably as important as the direct benefits of reserves to developing areas of the world. It remains to be seen whether successful reserves such as Apo Reserve have broader-scale direct benefits to fisheries through net larval export.

Acknowledgments

This project was funded by a Pew Fellowship in Marine Conservation and an Australian Research Council Grant (DP0209086) to G. R. Russ and A. C. Alcala. Travel to the Philippines for R. A. Abesamis was funded by the Australian Agency for International Development (AusAID). We thank Analie Candido, Mary Aldeon, Francia Candido, and Olivia Alaton for invaluable assistance in the collection of data. The Apo Island Protected Area Management Board, Aileen Maypa, Hilconida Calumpong, and staff at SUAKCREM are acknowledged for logistical assistance.

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Comparing the identification of southern California juvenile rockfishes (genus *Sebastes* spp.) by restriction site analysis of the mitochondrial ND3/ND4 region and by morphological characteristics

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Abstract—Rockfish (*Sebastes* spp.) juveniles are often difficult to identify by using morphological characters. This study independently applies morphological characters and a key based on mitochondrial restriction site variation to identify juvenile rockfishes collected in southern California during juvenile rockfish surveys. Twenty-four specimens of *Sebastes* were examined genetically without knowledge of the morphological assignment. Seventeen fish were identified genetically as *S. semicinctus*, *S. goodei*, *S. auriculatus*, *S. jordani*, *S. levis*, *S. rastrelliger*, and *S. saxicola*. Identities for the remaining fish were narrowed to two or three species: 1) three fish were either *S. carnatus* or *S. chrysomelas*; 2) one fish was either *S. chlorosticus*, *S. eos*, or *S. rosenblatti*; and 3) three fish could have been either *S. hopkinsi* or *S. ovalis*, the latter for which we now have distinguishing mitochondrial markers. The genetic and morphological assignments concurred except for the identity of one fish that could only be narrowed down to *S. hopkinsi* or *S. semicinctus* by using morphological characters. Genetics excluded more species from multispecies groupings than did the morphological approach, especially species within the subgenus *Sebastomus*. Species in the genetically unresolvable groups may be similar because of recent divergence or because of interspecies introgression.

Manuscript submitted 11 October 2004 to the Scientific Editor's Office.

Manuscript approved for publication 21 September 2005 by the Scientific Editor.

Fish. Bull. 104:376–382 (2006).

Sixty-five rockfish species (*Sebastes* spp.) inhabit the waters along the California coast (Moser, 1996). Within the genus, there is a high degree of similarity among many species in morphological characters. These similarities are in part due to recent divergence, but may also have resulted from convergence of congeners occupying similar habitats. Identification of *Sebastes* (and most species) is usually based on morphology; however, this approach may fail, especially for identifying sympatric species, which can be similar in coloration and overlap in morphological characters. Juvenile rockfishes are morphologically distinct from larvae and adults (Kendall, 2000), and juvenile stages of many species, especially the pelagic juvenile stage, have not yet been described; only a few species have complete ontogenetic descriptions (Matarese et al.,1989; Moser, 1996). The species of a few *Sebastes* larvae can be determined and adults can be misidentified.

Rockfishes are important ecologically and some species are economically valuable. *Sebastes* larvae are a large component of ichthyoplankton collections and rank third or fourth in abundance among all fish larvae taken during California Cooperative Fisheries Investigations (CalCOFI) surveys, which cover the entire length of the California and Baja California coast and now survey southern California. The ability to identify *Sebastes* accurately and efficiently at all developmental stages will, in turn, greatly increase our knowledge of their life histories, as well as our management and conservation efforts. An increased understanding of life history variation can improve the systematic descriptions of *Sebastes* species, which have mostly been based on the morphology of adults.

The analysis of restriction site variation of polymerase chain reaction (PCR)-amplified mtDNA is an effective and relatively simple method for species identification of adult specimens of fish species. The use of restriction enzymes to cleave the DNA can reveal variation in the mtDNA sequence at specific sites, and individuals or species can often be distinguished by the presence or absence of these sites. This method has advantages over sequencing in that it can be conducted relatively easily and used to survey large stretches of a DNA sequence, whereas sequencing,

because of its high cost, is usually limited to a much smaller span of DNA. Closely related species of several genera have been identified with this method; for example, snappers (Chow et al., 1993), eels (Aoyama et al., 2000; Lin et al., 2002), billfishes (Innes et al., 1998), and rockfishes (Gharrett et al., 2001). For identification of larvae and juveniles, restriction site patterns of adults can be used as references to ensure the reliability of the results. A limited database was used and a small number of samples were tested for a previous report on larval and juvenile identification of *Sebastes*, also based on restriction patterns of the mtDNA (Taylor, 1998).

The objective of this study was to compare the results of identifying pelagic juvenile rockfishes by the application of a key for delineating species based on mtDNA variation of adult rockfishes (Li et al., 2006) and by using only morphological characteristics. The questions we addressed were the following: Are the results for both genetic identifications and morphological identifications concordant? If not, how did these two methods differ? The targets of the comparison were samples of pelagic juvenile rockfishes collected from southern California. Both genetic and morphological analyses were conducted without knowledge of the results of the other.

Table 1

Sample identification numbers, sampling location, standard length (SL), weight, and method of tissue storage of juvenile specimens of *Sebastes* spp. Missing sample numbers are those for which the DNA could not be amplified: a = frozen on the boat, thawed on ice when genetic material was taken; b=put into ethanol on the boat.

Sample number	North latitude	West longitude	SL (mm)	Weight (g)	Preservation technique
1	34.20	120.24	41.3	1.200	a
2	"	"	42.2	1.282	a
3	"	"	35.8	0.756	a
4	"	"	36.1	0.777	a
5	"	"	31.0	0.478	a
8	"	"	29.5	0.360	a
9	"	"	24.1	0.206	a
15	34.26	120.15	28.9	0.265	b
16	"	"	37.6	0.565	b
17	"	"	34.0	0.654	b
18	"	"	23.2	0.150	b
19	"	"	26.0	0.326	b
20	"	"	35.1	0.591	b
21	"	"	24.8	0.273	b
22	"	"	22.6	0.190	b
23	"	"	21.0	0.140	b
25	"	"	25.0	0.273	b
26	34.23	119.93	27.6	0.472	b
27	"	"	26.8	0.235	b
31	"	"	28.0	0.345	b
44	"	"	37.9	0.799	b
45	"	"	35.6	0.590	b
48	"	"	24.2	0.189	b
49	"	"	24.3	0.168	b

Materials and methods

Collection of juveniles

Juvenile rockfishes were collected from the coast of Santa Barbara, California in June of 1998 and 2000 (Table 1). Fish were captured at night with a modified Cobb mid-water trawl with a nominal 12.2 m×12.2 m opening and 9-mm mesh net. Average trawling depth ranged from 18 to 29 m below the surface and above bottom depths ranged from 500 to 800 m, except for one specimen that was caught over a bottom depth of 88 m. Generally, specimens were sorted and then frozen on board the vessel. However, specimens from two hauls were sorted and immediately put in 95% ethanol aboard the vessel. Similar collection methods were used for both years. Details of the 1998 survey are provided in Nishimoto and Washburn (2002). The standard lengths (mm) of the specimens ranged from 16 to 42 mm.

Genetic identification

Following collection, each fish was identified in the laboratory by using morphological characters and meristics and pigmentation patterns. Specimens were chosen for genetic examination based on morphological differences. Fish representing different developmental stages (e.g., transition from larval to pelagic juvenile stage) of a species were included in the sample. We examined forty-nine specimens that included species that were easily identified based on pigmentation and morphological characters and individuals for which identification was less certain. All specimens were provided for genetic analysis without information on the morphological assignment.

For the genetic analysis, muscle tissue and skin from one side of the body was removed from each specimen in September 2000. Total genomic DNA was isolated by using a Purgene DNA™ isolation kit (Gentra Systems, Inc., Minneapolis, MN). Total DNA of each specimen was PCR-amplified and digested with specific restriction enzymes as directed in the key (Li et al., 2006). In some cases, digests with additional restriction enzymes were conducted to increase certainty of the identifications. Restriction fragments were separated electrophoretically on 1.5% agarose gels (one part agarose [Sigma-Aldrich, St. Louis, MO] and two parts Synergel™ [Diversified Biotech Inc., Boston, MA]) in 0.5×TBE buffer (TBE is 90 mM Tris-boric acid, and

Table 2

The most commonly occurring count (majority) and range of counts of dorsal-, anal-, and pectoral-fin rays among adults of *Sebastes* spp. identified in this study and for species that have morphologically similar pelagic juveniles or that are yet undescribed. (Compiled from Laidig and Adams, 1991; Moser, 1996; Love et al., 2002). Grouping of species is explained in the text.

	Dorsal-fin rays		Anal-fin rays		Pectoral-fin rays	
Species	Majority	Range	Majority	Range	Majority	Range
Species with distinct morphological characteristics						
S. levis	12–13	12–13	7	6–7	18	17–18
S. goodei	14	13–16	8	7–9	17	16–18
S. jordani	14–15	13–16	9–10	8–11	20–21	19–22
Group I						
S. saxicola	12	11–14	7	5–8	16	15–18
S. rastrelliger	13	12–14	6	6	19	18–20
S. semicinctus	13	12–14	7	6–8	17	16–18
S. auriculatus	13	12–15	7	5–8	18	15–19
S. wilsoni	13–14	13–15	6	5–7	17	16–18
S. hopkinsi	14–15	13–17	7	6–9	17	16–18
S. ovalis	14–16	13–16	8–9	7–9	18	17–19
Group II						
S. caurinus	12–13	11–14	6	5–7	17	16–18
S. carnatus	13	12–14	6	5–7	17	16–18
S. chrysomelas	13	12–14	6	5–7	17	17–18
S. atrovirens	14	12–15	7	6–8	17	16–18
Sebastomus group						
S. rosenblatti	12	11–13	6	5–6	17	16–18
S. lentiginosus	12	12–13	6	6–7	17	16–18
S. eos	12–13	11–13	6	5–7	17–18	16–18
S. umbrosus	12–13	11–14	6	5–7	16–17	15–18
S. rosaceus	12–13	11–14	6	5–7	17	16–18
S. chlorostictus	12–13	11–15	6	5–7	17	16–18
S. helvomaculatus	13	12–14	6	5–7	16–17	15–18
S. constellatus	13	12–14	6	5–7	17	16–18
S. ensifer	13	12–14	6	5–7	17	16–18
S. simulator	13	12–14	6	5–6	17	16–18

2 mm EDTA, pH 7.5). A 100 base-pair (bp) ladder provided molecular weight markers to estimate restriction fragment sizes. Gels were stained with ethidium bromide and photographed on an ultraviolet light transilluminator. Restriction fragments that could not be accurately measured from agarose gels were separated on 8% polyacrylamide gels and stained with SYBR Green I Nucleic Acid Stain™ (Molecular Probes, Eugene, OR) by using a 25-bp ladder for a molecular weight standard. Successful PCR amplification was obtained from 24 of the specimens. A key based on restriction site variation (Li et al., 2006) was used in the identification of the rockfish specimens.

Morphological identification

Some of the pelagic juveniles included in this study could be identified from body and fin pigment patterns and from gross morphological characteristics, whereas others had not yet developed species-specific characters. Meristics used to identify rockfish species included counts of dorsal, anal, and pectoral fin rays (Table 2). Key gross morphological characteristics have been described for *S. jordani* (Moser et al., 1977), *S. levis* (Moser et al., 1977), *S. goodei* (e.g., 35.6-mm-SL specimen illustrated in Sakuma and Laidig [1995]), *S. semicinctus* (Laidig and Adams, 1991), *S. saxicola* (e.g., 38.2-mm-SL specimen illustrated in Laidig et al. [1996]), and *S. auriculatus* (Moser, 1996). However, recently transformed pelagic juveniles of the latter three species do not yet possess distinguishing pigmentation patterns. Those species are included in group 1 in Table 2 and require both morphological and meristic examinations to distinguish them. Although the fin spines of transforming pelagic juveniles are not fully ossified, counts of dorsal-, anal-, and pectoral-fin rays can be made and are useful for separating similarly pigmented species. Body shape, color, and the presence or absence of certain head spines

Table 3

Restriction fragment patterns and consequent species assignments, and species assignments based on morphological features for *Sebastes* spp. examined. Haplotypes a_1 and a_2 are variants of *Mbo* I haplotype a, which was first observed in the present study.

Sample	*Bst*N I	*Bst*U I	*Cfo* I	*Dde* I	*Hin*d II	*Hin*f I	*Mbo* I	*Msp* I	*Rsa* I	Genetic assignment	Morphological assignment
1	X		D		A	C	p			*S. semicinctus*	*S. semicinctus*
2	Z		A		A	g	K			*S. hopkinsi* or *ovalis*	*S. hopkinsi*
3	Z		A				K			*S. hopkinsi* or *ovalis*	*S. hopkinsi*
4	Z		A			g	g			*S. hopkinsi*	*S. hopkinsi*
5	Z						g			*S. hopkinsi*	*S. hopkinsi*
8	X						p			*S. semicinctus*	*S. semicinctus*
9	Z									*S. hopkinsi*	*S. hopkinsi* or *semicinctus*
15	Y		D			O	a_1		E	*S. goodei*	*S. goodei*
16	Y		D			O	a_2		E	*S. goodei*	*S. goodei*
17	O	C	D			G	f		C	*S. saxicola*	*S. saxicola*
18	a						c			*S. jordani*	*S. jordani*
19	B					A	q			*S. levis*	*S. levis*
20	Z		A			g	K		C	*S. hopkinsi* or *ovalis*	*S. hopkinsi*
21	c		C	v		a	A		B	*S. rastrelliger*	*S. rastrelliger*
22	F		A	i	C	G	C	a	B	*S. carnatus* or *chrysomelas*	*S. carnatus* or *chrysomelas*
23	F		a	i	C	G	C	a	B	*S. carnatus* or *chrysomelas*	*S. carnatus* or *chrysomelas*
25	F		A	i	C		C	a	B	*S. carnatus* or *chrysomelas*	*S. carnatus* or *chrysomelas*
26	F		D			A	E		C	*S. chlorostictus* or *eos* or *rosenblatti*	*Sebastomus*
27	X		D			C	p			*S. semicinctus*	*S. semicinctus*
31	F		D	v	A	A	k		B	*S. auriculatus*	*S. auriculatus*
44	Z		A	n		g	K		C	*S. hopkinsi*	*S. hopkinsi*
45	Z		A			g	g		C	*S. hopkinsi*	*S. hopkinsi*
48	Z			n			K			*S. hopkinsi*	*S. hopkinsi*
49	X						p			*S. semicinctus*	*S. semicinctus*

(as in the case of *S. auriculatus*) can help to differentiate species with overlapping meristic ranges.

Species that could not be identified from their morphological features were assigned to a complex of species or a subgenus. Group 2 in Table 2 includes species that have similar pigmentation patterns during their pelagic juvenile stage. Meristics and head spination are used to identify *S. atrovirens*. However, the remaining three, *S. carnatus*, *S. caurinus*, and *S. chrysomelas*, are assigned as a species complex because of the uncertainty in identifying the species. The subgenus *Sebastomus* includes ten rockfish species that were found in the collection area and that cannot be distinguished by morphological characters and meristics or by pigmentation.

Results

The way in which the specimens were handled and preserved affected DNA quality and limited the number of genetic and morphological species assignments that could be compared. Only the DNA of seven of the 25 specimens frozen at sea and later thawed and processed was successfully amplified, whereas the DNA of 17 of the 24 specimens preserved in 95% ethanol at the time of capture was amplified. A total of 24 specimens were identified to species or species group based on restriction fragment patterns of the mtDNA using one or more restriction endonucleases (Table 3) and without knowledge of the morphological assignment. Table 4 sum-

Table 4

Developmental stages and counts of dorsal rays, anal rays, and pectoral rays used to assign species to *Sebastes* samples that were independently identified through **genetic analysis.** The number of specimens is given in parentheses. * indicates that the paired fins differed.

Morphological assignment	Genetic assignment	Number of samples	Developmental stage	Number of dorsal rays	Number of anal rays	Number of pectoral rays*
S. auriculatus	*S. auriculatus*	1	juvenile	13	7	18
S. carnatus, *chrysomelas*, or *caurinus*	*S. carnatus* or *chrysomelas*	3	transforming juvenile (3)	12(2), 13(1)	6(3)	17(3)
S. goodei	*S. goodei*	2	transforming juvenile (1), juvenile (1)	13(1), 14(1)	8(2)	17(2)
S. hopkinsi	*S. hopkinsi*	5	transforming juvenile (2), juvenile (3)	14(2), 15(2), 16(1)	7(5)	17(4), 17/18(1)
S. hopkinsi	*S. hopkinsi* or *ovalis*	3	juvenile (3)	14(1), 15(2)	7(3)	17(3)
S. jordani	*S. jordani*	1	transforming juvenile	14	9	20
S. levis	*S. levis*	1	transforming juvenile	13	6	18
S. rastrelliger	*S. rastrelliger*	1	juvenile	13	6	19
S. saxicola	*S. saxicola*	1	juvenile	12	6	16
subgenus *Sebastomus*	*S. chlorostictus*, *eos*, or *rosenblatti*	1	juvenile	12	6	18
S. semicinctus	*S. semicinctus*	4	transforming juvenile (2), juvenile (2)	13(4)	7(4)	17(2), 16/17(1), 18(1)
S. hopkinsi or *semicinctus*	*S. hopkinsi*	1	transforming juvenile	14	7	17

marizes the meristic data used to identify species morphologically. When a fish could not be assigned to a species, it was assigned to a species complex or subgenus.

The individuals genetically identified to species were six *S. hopkinsi*, four *S. semicinctus*, two *S. goodei*, one *S. auriculatus*, one *S. jordani*, one *S. levis*, one *S. rastrelliger*, and one *S. saxicola*. The restriction fragment patterns of these juveniles were identical to those of previously observed adult specimens, except for the two *S. goodei* juveniles, each of which differed by a single difference (presumably a site loss in one fish and a site gain in the other) from reference specimens for *Mbo* I (Table 3 and Li et al., 2006). The genetic species assignment of all but one of these specimens matched the identification based on morphological characters (Table 4). The discrepant fish was identified morphologically as either *S. semicinctus* or *S. hopkinsi*. The specimen had 14 dorsal rays, which is within the range of both species (Table 2) and was a transforming pelagic juvenile that had not yet developed the discernible body pigmentation pattern of older juveniles (Table 4).

At the beginning of the study, *S. ovalis* was not included in our database. When we added restriction site information for *S. ovalis* to the database, we found that the species is very similar to *S. hopkinsi* in its haplotype profile. Consequently, three individuals morphologically identified as *S. hopkinsi* were genetically assigned to the complex *S. hopkinsi-S. ovalis*. The restriction enzyme *Dde* I can delineate the two species; however, when we discovered the ambiguity, no samples remained for analysis. Based on meristics, the three specimens are more likely *S. hopkinsi* than *S. ovalis*. The range of counts for fin rays overlaps for the two species (Table 2). However, *S. ovalis* commonly has eight or nine anal rays, and the three specimens in question possessed seven rays that occur commonly in *S. hopkinsi* (Table 4).

Three specimens were assigned to the species complex *S. carnatus-S. chrysomelas-S. caurinus* according to morphological criteria. Haplotype information eliminated *S. caurinus*. Genetic analysis of the one specimen that was morphologically assigned to the subgenus *Sebastomus*, which includes 13 North Pacific species, reduced the possible species to *S. chlorosticus*, *S. eos*, or *S. rosenblatti*.

Discussion

Our results demonstrated that restriction site analysis of mtDNA is a simple and effective tool for identifying juveniles of *Sebastes*

species. The presumed intraspecific variation observed in *S. hopkinsi* and *S. goodei* did not interfere with the application of interspecific variation in species identification, and our other work (Gharrett et al., 2001; Li, 2004) indicates that intraspecific variation generally does not obscure delineation of species. The key we constructed for mtDNA restriction site variation can be especially helpful in learning about variation in the distinguishing morphological characters of the early life stages of *Sebastes*.

One factor that prevented identification of some juvenile specimens was poor DNA quality. Specimens must be properly preserved to provide high quality DNA for genetic analysis. Our success in amplifying DNA from specimens preserved in several volumes of 95% ethanol immediately after capture was substantially higher than that of specimens that had been frozen after capture and subsequently thawed for morphological studies.

Several small groups of species had similar restriction site patterns. Consequently, there was ambiguity in the genetic analysis of those groups. Specifically, we were unable to separate *S. carnatus* from *S. chrysomelas*, and we were unable to distinguish among *S. chlorostictus*, *S. eos*, and *S. rosenblatti*. However, morphological characteristics could not reveal a difference between *S. carnatus* and *S. chrysomelas*, nor could they distinguish any of the 13 *Sebastomus* species, including *S. chlorostictus*, *S. eos*, and *S. rosenblatti*.

Sebastes carnatus and *S. chrysomelas* are very closely related and, as adults, differ morphologically only in body coloration. *Sebastes carnatus* has flesh-colored blotches on an olive-brown background, and *S. chrysomelas* has yellow blotches on a black background (Love et al., 2002). They are found across similar geographic ranges, from northern California to Baja California, and are often sympatric, inhabiting rocky substrates, although they have different depth distributions (Larson, 1980), and their segregation is maintained by the social dominance of *S. chrysomelas* (Larson, 1980; Hoelzer, 1987). The two species may also differ slightly in gill-raker counts: *S. carnatus* typically has 28–30, and *S. chrysomelas* typically has 27–28 (Hallacher and Roberts, 1985). Their taxonomic status as distinct species is generally recognized from their different colorations, even though no fixed biochemical or genetic differences have been reported (Seeb, 1986; Seeb and Kendall, 1991; Hunter, 1994; Alesandrini, 1997). A recent study with the use of microsatellites in the nuclear DNA and mtDNA sequence variation has provided evidence that the two species *S. carnatus* and *S. chrysomelas* are genetically divergent (Narum, 2000).

Sebastes chlorostictus, *S. eos*, and *S. rosenblatti* are also morphologically similar, are present sympatrically, and are closely related (Chen, 1971; Love, 1996; Rocha-Olivares et al., 1999; Love et al., 2002). As adults, these species segregate by depth to some extent; *S. rosenblatti* occupies a somewhat narrower range than the other two (Love et al., 1990). Cladistic analyses indicate that *S. rosenblatti* is the most ancient of the three species (Rocha-Olivares et al., 1999). Estimates of divergence times of the subgenus *Sebastomus* may indicate that the three species are the result of the most recent speciation events within the subgenus, which may have begun less than 140,000 years ago (Rocha-Olivares et al., 1999).

The assignment of four specimens to multispecies groups in this study indicates the need for further effort to develop markers that will delineate the species in question. Approaches include screening additional regions of the mtDNA and application of additional restriction enzymes. If additional mtDNA regions and restriction enzymes do not provide species-specific information, other molecular techniques, such as the use of microsatellites, should be considered.

Acknowledgments

This work represents, in part, the master's thesis work of Z. Li at the University of Alaska Fairbanks. The project was supported by funding from the U.S. Geological Service (Biological Resources Division) Western Regional Office in Seattle, WA (R.W.O. 32) to AJG. Funding for MMN and MSL was provided by the Biological Resources Division under a cooperative agreement no. 1445-CA09-95-0836 with the Marine Science Institute, University of California, Santa Barbara.

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Abstract—Although bocaccio (*Sebastes paucispinis*) was an economically important rockfish species along the west coast of North America, overfishing has reduced the stock to about 7.4% of its former unfished population. In 2003, using a manned research submersible, we conducted fish surveys around eight oil and gas platforms off southern California as part of an assessment of the potential value of these structures as fish habitat. From these surveys, we estimated that there was a minimum of 430,000 juvenile bocaccio at these eight structures. We determined this number to be about 20% of the average number of juvenile bocaccio that survive annually for the geographic range of the species. When these juveniles become adults, they will contribute about one percent (0.8%) of the additional amount of fish needed to rebuild the Pacific Coast population. By comparison, juvenile bocaccio recruitment to nearshore natural nursery grounds, as determined through regional scuba surveys, was low in the same year. This research demonstrates that a relatively small amount of artificial nursery habitat may be quite valuable in rebuilding an overfished species.

Potential use of offshore marine structures in rebuilding an overfished rockfish species, bocaccio (*Sebastes paucispinis*)

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Manuscript submitted 2 September 2005 to the Scientific Editor's Office.
Manuscript approved for publication 26 September 2005 by the Scientific Editor.
Fish. Bull. 104:383–390 (2006).

Beginning in 1995, annual surveys of fish assemblages at oil and gas platforms and natural reefs throughout southern California were conducted with a research submersible (summarized in Love et al., 1999, 2000, 2003). Many California oil and gas platforms harbor three fish assemblages: those that occupy the shell mound area surrounding the base of the platform; those that occupy the waters adjacent to the platform bottom, and those that occupy the midwater. Rockfishes (genus *Sebastes*), of about 35 species, dominate these assemblages. The shell mound assemblage is composed primarily of juvenile rockfishes, dwarf rockfishes, and other species; the platform bottom assemblage is composed of adult and subadult fishes; and the midwater assemblage of most platforms (and the bottoms of some mid-depth platforms) is dominated by young-of-the-year (YOY) and older juvenile rockfishes that comprise at least 28 species. These fishes are rarely more than 20 cm long (total length). In the midwaters of most California platforms, there are only low densities of predatory reef fish species, such as kelp bass (*Paralabax clathratus*) and cabezon (*Scorpaenichthys marmoratus*), or semipelagic, large predatory species, such as Pacific barracuda (*Sphyraena argentea*) and yellowtail (*Seriola lalandi*). The proper disposition of the approximately 6000 marine offshore oil and gas platforms and associated structures now in service worldwide is in dispute. There are 27 platforms off California and, as in other parts of the world, there is considerable debate over the ultimate fate of these structures once they are uneconomical to operate (Schroeder and Love, 2004). In this article, we focus on the role that some artificial structures play as rockfish nursery habitat off California.

During some years, we have noted particularly high densities of YOY bocaccio (*Sebastes paucispinis*), widow (*S. entomelas*), squarespot (*S. hopkinsi*), and blue (*S. mystinus*) rock-

Figure 1

Examples of young-of-the-year (YOY) and other juvenile fishes found in high densities at platform Gilda, October 2003. (**A**) YOY bocaccio (*Sebastes paucispinis*); (**B**) a YOY lingcod (*Ophiodan elongatus*); (**C**) one-year-old vermilion rockfish (*Sebastes miniatus*).

fishes around a number of these platforms. Similar high densities of young rockfishes were noted in the late 1950s at two nearshore platforms off Santa Barbara (Carlisle et al., 1964). The densities of YOY rockfishes are usually higher at platforms than at most natural outcrops (Schroeder et al., 2000; Love et al., 2003). As on natural outcrops, however, YOY rockfish recruitment to platforms is highly variable from year to year.

In 2003, while conducting fish surveys around eight oil platforms in southern California, we observed high densities of YOY rockfishes (e.g., bocaccio and widow rockfish), YOY lingcod (*Ophiodon elongatus*), and one-year-old vermilion rockfish (*S. miniatus*) (Fig. 1). Given the uncertainty regarding the role that platforms might play as fish habitat, we were interested in understanding how important young bocaccio, and by extension the platforms, might be to the stock and populations of this species in the region. Because of the severely overfished status of bocaccio and because a stock assessment model had been developed by NOAA Fisheries, we focused our attention on this species.

Along the Pacific Coast of North America, bocaccio have been reduced to about 7.4% of their unfished population (MacCall[1]). Bocaccio are relatively long-lived (to over 50 years) and have extremely variable annual juvenile recruitment success; over natural outcrops, large year classes are found about once a decade (Tolimieri and Levin, 2005). YOY bocaccio settle from a juvenile micronektonic stage to shallow high-relief habitats (such as kelp beds) and usually migrate into deeper waters within one year. Historically, the species was abundant from Oregon to at least northern Baja California (Love et al., 2002).

In this article we focus on the large recruitment of YOY bocaccio observed at platforms in the Santa Barbara Channel in 2003. We estimate the minimum number of YOY bocaccio at eight platforms in the Santa Barbara Channel, southern California, and estimate the contribution these juveniles may make (as surviving adults) to the rebuilding of the overfished stock. We also compare the densities of YOY bocaccio around the platforms with those determined during the same year in studies on natural reefs throughout southern, and parts of central, California.

Material and methods

Between 10 and 15 October 2003, we surveyed the jacket (horizontal beams and vertical supports)

[1] MacCall, A. D. 2003. Status of bocaccio off California in 2003. *In* Status of the Pacific coast groundfish fishery through 2003 stock assessment and fishery evaluation (vol. 1), v+56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 200, Portland, OR 97220.

of eight platforms in the Santa Barbara Channel (Fig. 2) using the *Delta* research submersible, a 4.6-meter, 2-person vessel operated by Delta Oceanographics of Oxnard, California. In the platform midwater, we conducted surveys along each of the platform's horizontal beams, located at 20- to 30-m intervals between near-surface waters and the bottom. The shallowest beams were situated at depths of 15–34 m; thus the uppermost parts of the platform were not surveyed. On the seafloor, fish surveys were conducted next to the platform bottom and over the shell mounds that surround platforms. Because of poor water visibility, we were unable to survey either the platform bottoms or the shell mounds of four platforms (i.e., A, B, C, and Hillhouse). We conducted belt transects on the shell mound at an average distance of approximately 7.75 m from the platform and around the platform base and horizontal beams at a distance of approximately 2 m from the platform, while the submersible maintained a speed of about 0.5 knots. Divers estimated transect lengths by first estimating velocity over a short course, using twin laser beams as an aid to estimate their lengths. Submersible surveys were conducted during daylight hours between one hour after sunrise and two hours before sunset. During each transect, the researcher made observations from a viewing port on the starboard side of the submersible. An externally mounted hi-8-mm video camera with associated lights filmed the same viewing fields as seen by the observer. Images recorded by the camera were laid down on tape. The observer identified, counted, and estimated the lengths of all fishes and verbally recorded those data on the videotape. All fishes within two meters of the submersible were counted. Fish lengths were estimated by using a pair of parallel lasers mounted on either side of the external video camera. The projected reference points were 20 cm apart and were visible both to the observer and in the video camera image. We assumed that bocaccio 20 cm or less were YOY, in accordance with growth studies of bocaccio.

Many years of experience along the Pacific Coast have shown that if the *Delta* is moving at a constant and slow rate of speed, as in these surveys, there is very little obvious effect on most fishes, particularly rockfishes (M. Love[2]; O'Connell[3]; Yoklavich[4]). Certainly, we noticed virtually no movement from most of the fishes in our study as the research submersible passed by. Unless hidden in complex substrate, fishes as small as about 5 cm in length are readily visible within two meters of the submersible.

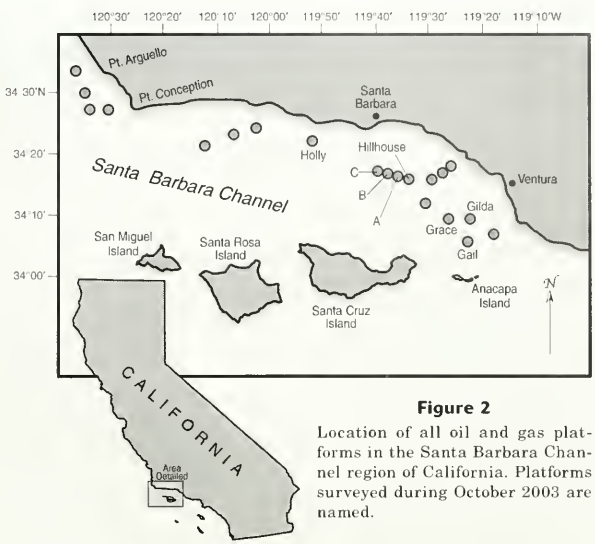

Figure 2

Location of all oil and gas platforms in the Santa Barbara Channel region of California. Platforms surveyed during October 2003 are named.

Using the data from these surveys, we computed the densities (number of fish per m^2) of YOY bocaccio at the midwater horizontal beams, bottom (when surveyed), and shell mounds (when surveyed) of each platform. From these density estimates, we calculated the abundance of YOY bocaccio at each platform (for protocols see Love[5]).

These abundance estimates are conservative for four reasons. First, we conducted the platform surveys about two meters from the platform and our belt transects count only those YOY bocaccio within two meters of the submersible. Particularly in platform midwaters, densities of YOY rockfishes tend to be lower outside the platform framework (the zone traversed by the submersible) than inside. Second, beginning a few months after settling on platforms, the more open water species, such as bocaccio, blue, widow, squarespot, and yellowtail rockfishes, become less closely associated with structure. There appears to be an ontogenetic shift away from a close association with habitat to a wider association, where these fish wander away from the immediate vicinity of the platform. This shift is particularly true during years with high densities (as in 2003), when large schools wander freely within the relatively open waters of the platform jacket. Third, as noted above, at each

[2] Love, M. 2002. Unpubl. data. Marine Science Institute, University of California, Santa Barbara, CA, 93160.

[3] O'Connell, V. 2004. Personal commun. Alaska Department of Fish and Game, 304 Lake St. Room 103 Sitka, AK 99835.

[4] Yoklavich, M. 2004. Personal commun. NOAA/NMFS Santa Cruz Laboratory, 110 Shaffer Road Santa Cruz, CA 95060.

[5] Love, M. 2005. Methods used to estimate abundance in numbers of young-of-the-year (YOY) bocaccio. Website: http://www.id.ucsb.edu/lovelab [accessed on 26 September 2005].

platform we did not survey in the midwaters above the shallowest horizontal beam (at depths of 15–34 m). Thus, some of the potential bocaccio nursery grounds were not sampled. Fourth, for those platforms where visibility was too poor for us to sample the bottom or shell mound (A, B, C, and Hillhouse), we estimated YOY bocaccio abundances only for that part of the platform (the midwater) that could be surveyed. However, although visibility was too poor to conduct operations on the bottom, we could see high densities of bocaccio inside the platform below the submersible at several platforms when we conducted midwater surveys. Thus, on these platforms, it is highly likely that the YOY bocaccio aggregation extended well below the level of our surveys and that these aggregations contained substantially more of these fishes than we estimated.

We also estimated the level of recruitment of YOY bocaccio in 2003 to natural reefs using data from a variety of sources. In this overview, we included 1) our submersible surveys conducted at depths at which YOY bocaccio may reasonably recruit (down to about 100 m), 2) a scuba survey conducted by D. M. Schroeder, and 3) data from nearshore rocky reef fish surveys conducted by other researchers. The latter surveys were conducted by using scuba at depths of 25 m or less.

Table 1

Densities of young-of-the-year bocaccio (*Sebastes paucispinis*) at eight platforms in the Santa Barbara Channel, October 2003. Because of poor visibility, the zones of some platforms were not surveyed; these are marked N/A.

Platform	Platform zone surveyed	Depth (m)	Number of fish	Density (fish/100 m^2)
A	midwater	15	0	0
		32	0	0
	no base or shell mound	N/A	N/A	N/A
B	midwater	20	0	0
		30	13	4.8
		40	165	57.7
	no base or shell mound	N/A	N/A	N/A
C	midwater	20	0	0
		30	62	17
		45	127	32.1
	no base or shell mound	N/A	N/A	N/A
Gail	midwater	32	2	0.6
		47	27	6.7
		69	18	4.1
		90	3	0.8
		111	25	5.6
		138	1	0.2
		164	1	0.2
		195	4	0.7
	base	226	0	0
	shell mound	226	0	0
Gilda	midwater	25	55	13
		42	24	6.2
	base	62	1023	242.4
	shell mound	62	1078	169.6
Grace	midwater	26	4006	476.8
		45	1537	193.1
		68	1124	258
		70	845	171
		80	92	221.5
	base	96	13	2.6
	shell mound	96	0	0
Hillhouse	midwater	20	0	0
		35	506	140
	no base or shell mound	N/A	N/A	N/A
Holly	midwater	34	18	4
	base	60	12	2.1
	shell mound	60	4	0.4
Total			10,785	

Results

YOY bocaccio were observed at seven of the eight platforms we surveyed. We observed a total of 10,785 YOY bocaccio in the survey (Table 1). We saw no YOY bocaccio at depths of 20 m and less, none at 226 m, and relatively high densities at depths between about 25 and 80 m. Mean YOY bocaccio densities varied between platforms. Platform Grace (368.0 fish/100 m^2) and Gilda (95.2 fish/100 m^2) harbored the highest densities, whereas no YOY bocaccio were observed at Platform A (Fig. 3). Using the methods detailed in Love,[5] we estimated that there was a minimum of 433,682 YOY bocaccio at the seven platforms (Table 2).

Using the model STATC (details of the model are given in MacCall[1]), which is the current basis for fishery management under the Pacific Fisheries Management Council, we determined that the 433,682 YOY bocaccio living around these platforms constitute about 20% of

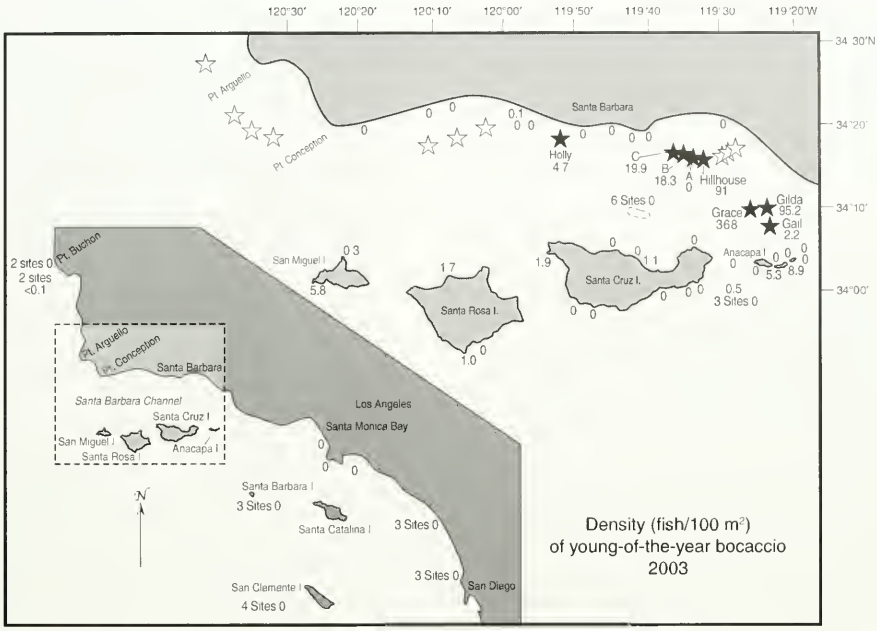

Figure 3

Densities of YOY bocaccio (*Sebastes paucispinis*) (fish/100 m^2) in southern and parts of central California in 2003. Surveys were conducted at sites that were likely YOY bocaccio recruitment habitats, primarily at nearshore kelp beds and rocky outcrops. Surveys by M. Love were conducted from the research submersible *Delta*; the others were conducted by scuba divers. The open stars represent platforms that were not surveyed; the closed stars represent platforms that were surveyed.

the average yearly value, and 40% of the median value for the entire range of the species (based on YOY estimated abundances between 1990 and 2003). From the same model, we estimated that these young fish will eventually contribute slightly less (0.8%) than one percent of the additional amount of fish needed to rebuild the Pacific Coast stock.

By comparison with most of the platforms we surveyed, there was low or no YOY bocaccio recruitment to natural reefs in southern and parts of central California during 2003 (Fig. 3). During 2003, surveys were conducted at 64 sites and no YOYs were observed at 50 of these reefs; most of the other 14 sites harbored very low densities. The highest density noted at any natural outcrop (8.9 fish/100 m^2), observed at a small kelp bed at Anacapa Island, was much lower than that at five of the surveyed platforms.

Table 2

Estimated numbers of young-of-the-year bocaccio (*Sebastes paucispinis*) inhabiting eight platforms in the Santa Barbara Channel, 2003. Note that the surveys of four platforms, Hillhouse, C, B, and A, did not include the bottom of the platform and its surrounding shell mound.

Platform name	Estimated abundance
Grace	353,411
Gilda	39,854
Hillhouse (partial)	22,171
C (partial)	5977
B (partial)	5911
Gail	5521
Holly	837
A (partial)	0
Total	433,682

Discussion

According to our estimates, the YOY bocaccio living around seven platforms in the Santa Barbara Channel were important to the regional bocaccio population, and it appears that a substantial portion of the YOY bocaccio

recruitment that occurred in the Santa Barbara Channel during 2003 took place at the surveyed platforms.

Because it is likely that most reefs both attract and produce fishes, discussions of reef function have evolved from the single issue of attraction versus production to an evaluation of the ecological performance of fishes at natural and human-made habitats. Reviews and studies that compare natural and human-made reefs as juvenile fish habitats should address: 1) a comparison of the survival rate of young fishes (including predation, growth rates, and survival after emigration, if that occurs) at the two habitat types, 2) the density of recruiting juveniles at a human-made reef versus that at surrounding natural reefs, 3) the possibility that a human-made reef is drawing recruiting juvenile fishes from nearby natural reefs, 4) the source of juvenile fishes found on a human-made reef—either from the plankton or from natural reefs (discussed in a number of papers including Bohnsack et al., 1994; Carr and Hixon, 1997; Pickering and Whitmarsh, 1997).

What is the survival rate of young fishes that recruit from the plankton to platforms and those that recruit to natural reefs? What appears to be a unique feature of the midwaters of many California platforms (compared to both natural reefs and to Gulf of Mexico platforms) is that many may act as juvenile (particularly YOY) fish refuges. The midwaters of platforms do not act as structural refuges. That is, they are not dotted with crevices, caves, and other complexities that allow fish to hide (Hixon and Beets, 1993). Rather, platforms may afford spatial refuges because, in general, concentrations of adult reef fishes tend to be found at the bottom of platforms (except for those platforms that harbor almost no adult fishes at all) rather than in the midwaters. Transitory and migrating piscivorous species, such as jacks and barracuda (taxa that are abundant around Gulf of Mexico platforms [Stanley and Wilson, 2000]) are also not common around most California platforms (Love et al., 2003). We have also not observed high densities of either fish-eating pinnipeds or sea birds around these structures. In addition, studies (Schroeder et al., 2005) demonstrate that predation rates on small fishes are lower in platform midwaters than at natural reefs.

Several lines of evidence demonstrate that YOY bocaccio recruit to platforms from the plankton and that the platforms do not attract previously settled fish from natural reefs. Studies of the seasonal timing of platform recruitment pulses and the size of the recruiting individuals are consistent with the hypothesis that young bocaccio settle on the platforms from the pelagic environment (Nishimoto et al., 2005; Schroeder[6]; Nishimoto[7]). Are these platforms, then, drawing away pelagic juveniles that would have settled instead on natural outcrops? Although it is possible that some pelagic juveniles that had settled on platforms would have found natural reefs, it is likely that most of these fish would not have survived in the absence of these structures. As an example, Emery et al. (2006) simulated near-surface drift trajectories from high-frequency radar current measurements to model movements of pelagic juvenile bocaccio in the vicinity of a platform off Pt. Arguello, central California. They estimated that for 1999 and 2002, a minimum of 76% and 69% of the modeled pelagic juvenile bocaccio would not have found natural habitat on which to settle. Although the platforms we surveyed were east of the platform examined in the Emery et al. (2006) study, it is unreasonable to conclude that these relatively small platforms are filtering the majority of pelagic juvenile bocaccio from the pelagic environment to the exclusion of natural reefs. Rather, it is possible that some platforms provide recruitment habitat for fishes that would otherwise be lost from the population.

What is the fate of YOY bocaccio that settle around platforms? In general, YOY bocaccio emigrate from shallower platforms within two years. At least some of these fish migrate to natural reefs, because young bocaccio tagged around Platforms A and B in 1978 and 1979 were recaptured on natural reefs as adults as much as 150 km from the tagging sites (Hartman, 1987). Our observations of bocaccio on the deeper Platform Gail demonstrate that many of the YOY bocaccio that recruited to that platform from the plankton in 1999 remained in the area (migrating to the bottom in 2000) and matured into adults (Fig. 4).

To summarize, the weight of evidence implies that some of the platforms in southern California produce bocaccio. During some years, young bocaccio settle from the plankton to the platforms in large numbers. This settlement may occur even when juvenile recruitment to natural reefs in the same region is low. Compared to the structure of most natural reefs, the structural complexity and high vertical profile of platforms probably provide pelagic juvenile rockfishes with a relatively strong stimulus to trigger settlement. Mortality on platform YOY bocaccio from predation may be relatively low because of a relative scarcity of predators. There is also evidence that platforms retain pelagic bocaccio juveniles that would otherwise have been carried into inhospitable offshore waters. At least some bocaccio that emigrate from platforms survive to populate natural reefs, whereas, as in the case of one platform, some YOY bocaccio remain and mature into adults. Thus, there is the likelihood that many of the YOY bocaccio we observed at platforms will either emigrate and seed natural reefs or will reside at the platforms and reproduce.

Clearly, our research was subject to a number of assumptions and the ambiguities that may be associated with these assumptions. These assumptions add some degree of uncertainty both to our estimates of YOY bocaccio abundances and their subsequent contribution to stock rebuilding. However, we consider this research to be sufficiently strong to demonstrate the importance of

[6] Schroeder, D. M. 2002. Unpubl. data. Marine Science Institute, University of California, Santa Barbara, CA 93106.

[7] Nishimoto, M. 2005. Personal commun. Marine Science Institute, University of California, Santa Barbara, CA 93106.

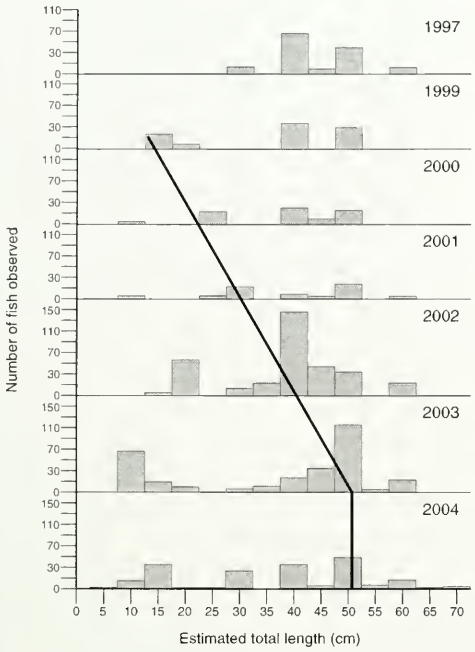

Figure 4

Size-frequency histogram of all bocaccio (*Sebastes paucispinis*) observed in all depths at Platform Gail from the research submersible *Delta*, 1995 to 2004. A relatively strong year class recruited in 1999 to the platform midwaters. We observed these fishes at the bottom in 2000 and they remained there through 2004. The near cessation of growth of these fishes between 2003 and 2004 approximates the size at which 100% of the fish are mature (Love et al., 2002).

spatial structure in driving marine population dynamics, where a small amount of nursery habitat, either human-made or natural, may disproportionately impact a widely distributed species. It also highlights the importance of understanding the potential role of any marine habitat before that habitat is altered, either purposefully or unintentionally.

Acknowledgments

This research was funded by the Biological Resources Division, U. S. Geological Survey (National Offshore Environmental Studies Program 1445-CA-0995-0386) based on an information need identified by the Minerals Management Service's Pacific OCS Regions, and by the California Artificial Reef Enhancement Program (CARE). We thank Jay Carroll, Matt Craig, David Huang, David Kushner, Brent Mardian, Dan Pondella, and Dan Reed for sharing their fish survey data with us. We thank the pilots of the submersible *Delta*, Chris Ijames, Joe Lily, and Dave Slater, for their very professional handling of the technical aspects of that survey, as well as the crews of the RV *Cavalier* and RV *Valero*. Linda Snook managed the survey data.

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Do oil and gas platforms off California reduce recruitment of bocaccio (*Sebastes paucispinis*) to natural habitat? An analysis based on trajectories derived from high-frequency radar

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Abstract—To investigate the possibility that oil and gas platforms may reduce recruitment of rockfishes (*Sebastes* spp.) to natural habitat, we simulated drift pathways (termed "trajectories" in our model) from an existing oil platform to nearshore habitat using current measurements from high-frequency (HF) radars. The trajectories originated at Platform Irene, located west of Point Conception, California, during two recruiting seasons for bocaccio (*Sebastes paucispinis*): May through August, 1999 and 2002. Given that pelagic juvenile bocaccio dwell near the surface, the trajectories estimate transport to habitat. We assumed that appropriate shallow water juvenile habitat exists inshore of the 50-m isobath. Results from 1999 indicated that 10% of the trajectories represent transport to habitat, whereas 76% represent transport across the offshore boundary. For 2002, 24% represent transport to habitat, and 69% represent transport across the offshore boundary. Remaining trajectories (14% and 7% for 1999 and 2002, respectively) exited the coverage area either northward or southward along isobaths. Deployments of actual drifters (with 1-m drogues) from a previous multiyear study provided measurements originating near Platform Irene from May through August. All but a few of the drifters moved offshore, as was also shown with the HF radar-derived trajectories. These results indicate that most juvenile bocaccio settling on the platform would otherwise have been transported offshore and perished in the absence of a platform. However, these results do not account for the swimming behavior of juvenile bocaccio, about which little is known.

Manuscript submitted 20 July 2004 to the Scientific Editor's Office.
Manuscript approved for publication 6 October 2005 by the Scientific Editor.
Fish. Bull. 104:391–400 (2006).

The 27 oil and gas platforms off southern and central California have limited life spans. Many of these structures have been in place for over 20 years (Love et al., 2003), and it is expected that some of these platforms will be decommissioned in the near future. Because decommissioning may entail full removal of the platform, agency personnel tasked with determining the best course of action in regard to the platforms would likely benefit from an understanding of the role that platforms play as fish habitat (Schroeder and Love, 2004).

The platforms harbor high densities of many species of fishes, although species compositions vary with platform bottom depth (Love et al., 1999a; 1999b; Love et al., 2003). About 35 species of rockfishes (genus *Sebastes*) dominate the three distinct assemblages found around many platforms in the Santa Barbara Channel and off central California: the bottom, shell mound, and midwater assemblages. Fishes around platform bottoms tend to be adult and subadult individuals. Those on the shell mounds are usually adults of dwarf species or juveniles of larger taxa. The midwater assemblages are composed almost entirely of juvenile fishes. Some of these juvenile fishes are one and two-year old individuals, but most are young-of-the-year (YOY) rockfishes. Densities of YOY rockfishes around platforms are usually far higher than those at nearby natural reefs (Love et al., 2003). These observations have raised a concern (e.g., Krop[1]).) that platforms

[1] Krop, L. 1997. Environmental user group representative, disposition panel. *In* Proceedings: Public workshop, decommissioning and removal of oil and gas facilities offshore California: recent experiences and future deepwater challenges, September 1997 (F. Manago, and B. Williamson, eds.), p 172. Mineral Management Service OCS Study 98-0023. Coastal Research Center, Marine Science Institute, Univ. California, Santa Barbara, California, 93106. MMS Cooperative Agreement Number 14-35-0001-30761.

may reduce recruitment to natural reefs by functioning as catchments for pelagic juvenile rockfishes.

To investigate the possibility that an oil platform may reduce recruitment of rockfishes to natural habitat, we simulated drift pathways (hereafter referred to as "trajectories") from an existing platform to nearshore habitat using current measurements from high-frequency (HF) radars.

Materials and methods

Species modeled

Because trajectories derived from HF radar approximate transport pathways of near surface water parcels, we chose to model the movements of pelagic juvenile bocaccio (*Sebastes paucispinis*) that dwell near the surface during their time in the plankton. This historically important recreational and commercial fishing target in central and southern California (Love et al., 2002), is also among the shallowest dwelling juvenile fishes (Lenarz et al., 1991; Ross and Larson, 2003).

Off central and northern California, parturition for bocaccio occurs from January to May and peaks in February (Love et al., 2002). Off southern California, the species has a reproductive season that spans all year, but most larvae are released from October to July, although January is the peak month. Juvenile bocaccio recruit to inshore waters from February to August off central California, although May through July is the peak season (Love et al., 2002). The trajectory simulation period from May through August was chosen to span this principal recruitment season.

Bocaccio range from the Alaska Peninsula to central Baja California, and adults are usually found over high relief boulder fields and rocks in 50–250 m of water (Love et al., 2002). The fish most often settle in rocky habitat covered with various algae or in sandy zones with eelgrass. Juvenile bocaccio are commonly found in drifting kelp (Mitchell and Hunter, 1970; Boehlert, 1977) indicating that the fish recruit to natural habitat encountered in offshore surface waters. For this analysis, we assumed that waters from the shallow subtidal to the 50-m isobath represented suitable habitat for juvenile recruits. This choice reflects the lack of information about suitable habitat locations in our study area and likely results in overestimates of the abundance of such habitat.

Annual scuba surveys and submersible surveys (1995–2001) in the Santa Barbara Channel and Santa Maria Basin regions showed that YOY bocaccio inhabit the upper 35 m around one or more platforms for each year surveyed. Platform Irene (34°36.62′N, 120°43.40′W; bottom depth 73 m) was selected for analysis because fish recruited to it each year from 1995–2001 (Love et al., 2001) and it was the site of the highest density of YOY bocaccio observed from submersible surveys during these years (Love et al., 2003). Moreover, from May through August, 1999 and 2002, Platform Irene was also in a region of good HF radar coverage, which allowed computation of extensive trajectory ensembles.

Ocean current measurement and trajectory calculation

Near-surface ocean currents were measured hourly by using an array of three HF radars (SeaSondes, manufactured by CODAR Ocean Sensors, Ltd. of Los Altos, CA) operating at 12–13 MHz. At these frequencies, the measurement is an average over the upper 1 m of the water column (Stewart and Joy, 1974). The radars were located at Pt. Sal, Pt. Arguello, and Pt. Conception (Fig. 1A). HF radars measure components of surface currents by means of a Doppler technique, at spatial increments of 1.5 km in range and 5° in azimuth from the radar location. Surface current vectors in an east-north coordinate system were computed on a 2-km grid by using the least square technique described by Gurgel (1994). With this technique, all current components obtained within a 3-km radius around each grid point were combined to estimate the surface current every hour. The 3-km radius limits the spatial resolution of the near-surface current fields. Emery et al. (2004) have described the processing of the HF radar data in more detail. Further discussion on the use of HF radars for measuring near surface currents is given by Paduan and Rosenfeld (1996) and Graber et al. (1997).

Emery et al. (2004) assessed performance of the three HF radars by comparing them with *in situ* current meters at 5 m depth. They found that root-mean-square differences in radial speed measurements between HF radars and current meters ranged from 0.07 to 0.19 m/s. Recent observations comparing surface currents from HF radars and drifters have indicated that differences are substantially reduced if spatial variability in current fields is accounted for (Ohlmann, 2005).

The areas used for computing trajectories were offshore of Pt. Conception and Pt. Arguello as shown in Fig. 2A for 1999 and Fig. 3A for 2002. These areas were selected to maximize the spatial coverage, and to minimize the inclusion of grid points with low temporal coverage. Variable coverage from individual radars results in differences in coverage between years. Boundaries of nominal coverage areas were oriented along and perpendicular to isobaths. Platform Irene is about 2 km from the inshore boundaries, which lie along the 50-m isobath (Figs. 2A and 3A). At times actual radar coverage exceeded nominal coverage boundaries as may be seen by comparing sample computed trajectories (black lines, Fig. 1A) with the 2002 boundary (gray closed curve, Fig. 1A). Coverage in 2000 and 2001 for May through August was inadequate for producing trajectory ensembles around Platform Irene.

A new trajectory was begun at the location of Platform Irene every 4 hours from 1 May through 31 August for 1999 and 2002. Positions along the trajectories were determined by integrating current vectors forward in time using a fourth order Runge-Kutta algorithm. Trajectories ended where they encountered spatial gaps or where they reached the edge of radar coverage.

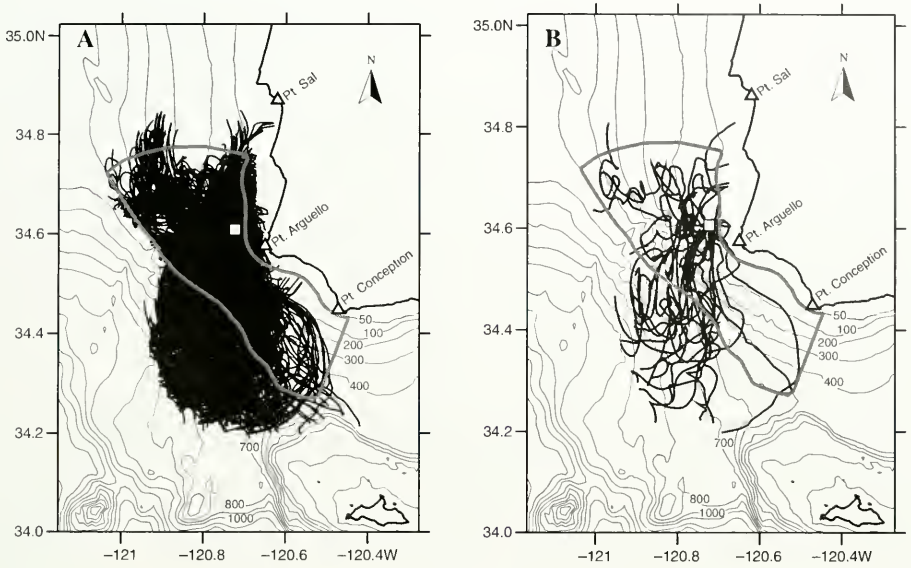

Figure 1

(**A**) Map of study area near Pt. Conception, California, showing trajectories derived from high-frequency (HF) radar from 1 May–31 Aug 2002. Triangles show HF radar locations and the white square shows Platform Irene. Gray curve superimposed on trajectories is the coverage boundary used for 2002. Labeled thin black lines are bathymetric contours. (**B**) Heavier black lines are 25 sample trajectories that intersect the coverage boundary. Gray curve is the same as in panel A. The trajectories in panels A and B were created from velocity time series that were interpolated with empirical orthogonal functions (EOFs).

The number of trajectories reaching the coverage boundaries defined in Figures 2A and 3A were reduced by gaps in spatial and temporal radar coverage. For example, of the 670 possible trajectories in 2002, 541 (81%) ended within the radar coverage area and 129 (19%) intersected the coverage boundary. Changes in spatial coverage on diurnal and longer time scales resulted from several factors, such as broadcast interference, and are a characteristic of HF radars (Paduan and Rosenfeld, 1996). Gaps in the velocity time series were also caused by outages of individual radars. The average durations of these gaps were 4.4 ±22.3 h and 5.9 ±7.9 h in 1999 and 2002, respectively. Outages of individual radars also produced a few long gaps in the velocity time series for each year across the entire coverage area. In 1999 two long gaps occurred: one from 1800 coordinated universal time (UTC) 28 June through 2000 UTC 22 July, and a second from 2300 UTC 24 July through 2200 UTC 13 August. In 2002 a single long gap occurred from 1700 UTC 16 May through 0100 UTC 21 May. These longer gaps were not filled.

Shorter gaps were filled by interpolation by using empirical orthogonal functions (EOFs; (Emery and Thomson, 1998)). EOFs incorporate the underlying spatial structure of all velocities recorded at all locations where data existed at a given time. Any velocity component, u say, at grid point j may be expressed as

$$u_j(t) = \sum_{i=1}^{N} a_i(t)\varphi_{ij} + \bar{u}_j, \quad (1)$$

where t = time;
$\bar{u}_j$ = the time average at location j (computed from available data at location j);
a_i = the time-varying amplitude function;
φ_{ij} = the ith spatial EOF mode at location j; and
N = the number of modes.

The first seven modes (i.e., N=7) were used for interpolation and explained 64% (1999) and 56% (2002) of the variance. EOF interpolation increases the number of trajectories reaching the coverage boundary to 99%. As a test, gaps were also filled with linear, spline, and moving average interpolation, but EOF interpolation resulted in the most trajectories reaching the coverage boundaries. Otherwise, results did not depend strongly on the interpolation method.

The fraction of filled data with EOF interpolation compared with the total possible data was 4% in 1999,

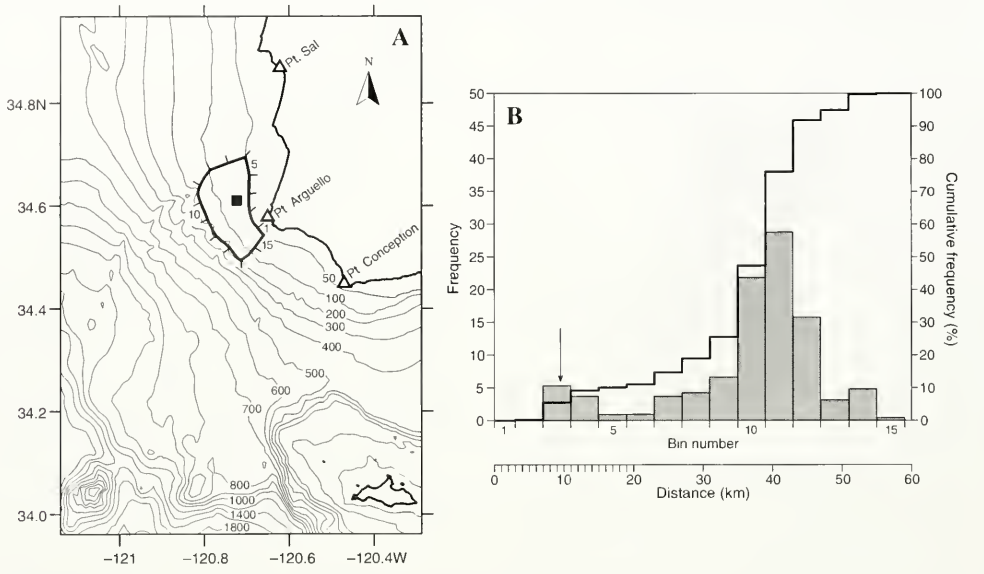

Figure 2

(**A**) Coverage boundary (indicated by heavy lines around the black square [Platform Irene]) for 1 May–31 August 1999. Numbers and tick marks around boundary identify bins corresponding to *x*-axis in panel B. (**B**) Histogram (gray bars, left-hand scale) and cumulative frequency (bold line, right-hand scale) show fraction of trajectories (in percent) intersecting bins around coverage boundary. Panel A shows bin locations. Distance around the coverage boundary (Fig. 2A) in kilometers is also shown (bottom scale). Arrow above histogram shows boundary location nearest Platform Irene.

12% in 2002, and 14% with the 2002 data for the 1999 coverage boundary. Here the total possible data were the number of grid points within the coverage boundary for either 1999 (45 grid points) or 2002 (291 grid points) multiplied by the number of hours between 1 May and 31 August minus the long gaps discussed above (2952 hours–1057 hours in 1999, 2952 hours–104 hours in 2002). Examples of 25 EOF-filled trajectories that started every 120 hours and intersected the 2002 coverage boundary are shown in Figure 1B.

The principal quantity used in our study to estimate how Platform Irene might affect transport to nearshore habitat was the histogram of points where trajectories crossed the boundaries of the coverage areas. To determine this quantity, coverage boundaries were divided into 4-km-long segments, or bins. The first bin of each histogram was less than 4 km because distances around the coverage boundaries were not exactly divisible by 4. Bin numbers increased counter-clockwise around the boundaries starting from 1 in the southeastern corner (Figs. 2A and 3A). The smallest numbers identified bins lying along the 50-m isobath.

Results

Trajectories originating at Platform Irene were sufficiently dense to fill in much of the surrounding area. In 2002 for example, EOF-filled trajectories spread over an area of about 20 km in the cross-shore direction by 60 km in the alongshore direction (Fig. 1A). North of Pt. Arguello, several trajectories crossed the 50-m isobath and some ended very near shore. South of Pt. Arguello, only a few trajectories approached the 50-m isobath. Instead, most turned southward or southwestward and moved offshore. A tendency for trajectories to align parallel to isobaths was evident in the northern end of the ensemble, although in other areas, such as the southeast, many trajectories lay across isobaths.

A histogram of points where trajectories crossed the coverage boundary for May–August 1999 exhibited a peak in bin 11 on the offshore side along the 500-m isobath (Fig. 2B, left-hand axis). Table 1 and the cumulative histogram (Fig. 2B, right-hand axis) showed that 76% of the trajectories crossed the offshore side corresponding to bin numbers 9–13. A second peak oc-

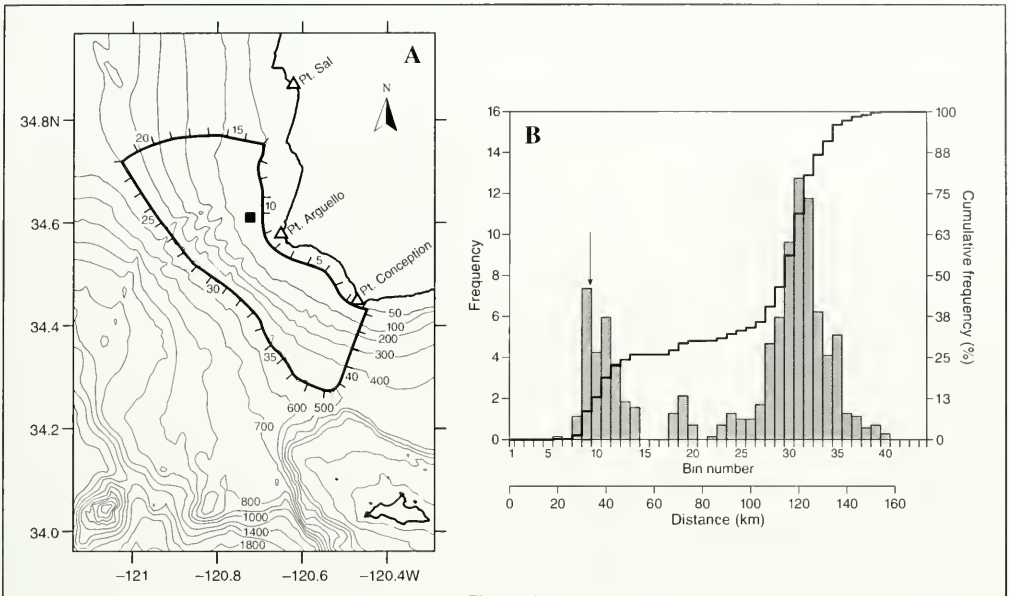

Figure 3

(**A**) Coverage boundary (indicated by heavy lines around the black square [Platform Irene]) for 1 May–31 August 2002. Numbers and tick marks around boundary identify bins corresponding to *x*-axis in panel B. (**B**) Histogram (gray bars, left-hand scale) and cumulative frequency (bold line, right-hand scale) show fraction of trajectories (in percent) intersecting bins around coverage boundary. Panel A shows bin locations. Distance around the coverage boundary (Fig. 2A) in kilometers is also shown (bottom scale). Arrow above histogram shows boundary location nearest Platform Irene.

Table 1

Statistics for trajectories using empirical orthogonal function (EOF) interpolation, and Scripps Institution of Oceanography drifters.

Year	Coverage boundary	Total trajectories	Trajectories intersecting coverage boundary	Trajectories intersecting inshore boundary (%) (50-m isobath)	Trajectories intersecting offshore boundary (%)	Trajectories intersecting northern boundary (%)	Trajectories intersecting southern boundary (%)	Mean residence time in coverage area (h ±1 SD)	Maximum residence time in coverage area (h)
1999	1999	590	546	10	76	9	5	19 (±12)	86
2002	2002	716	706	24	69	6	1	47 (±34)	163
2002	1999	716	712	18	66	7	8	22 (±18)	116
SIO drifters	2002	21	17	18	71	12	0	38 (±21)	79

curred in bin 3 and about 10% of trajectories crossed the inshore boundary on the 50-m isobath (bins 1–5). The remaining trajectories crossed either the northern (9%) or southern (5%) sides of the coverage boundary.

In 2002 the radars covered a substantially larger area (Fig. 3A), including about 50 km of the 50-m isobath, 70 km of the 500-m isobath along the offshore boundary, and a portion of the western entrance of the Santa Barbara Channel. The histogram of coverage boundary crossings for May–August 2002 also exhibited two peaks, one between bins 9–11 along the 50-m isobath and a second in bin 31 along the offshore side of the coverage boundary (Fig 3B). In 2002, 24% of trajectories crossed the 50-m isobath (bins 1–13), 69% crossed the

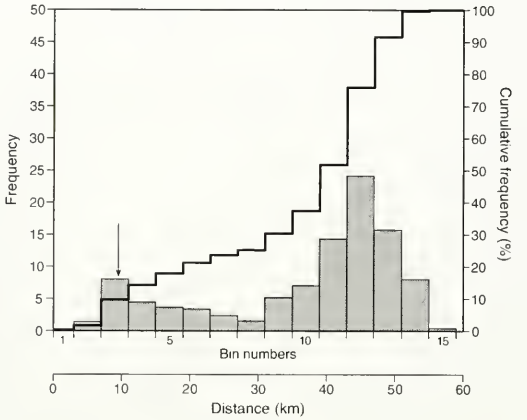

Figure 4

Histogram (gray bars, left-hand scale) and cumulative frequency (bold line, right-hand scale) showing percentage of 2002 trajectories intersecting bins from the 1999 coverage boundary. Bottom scale shows distance around the coverage boundary in kilometers. Arrow above histogram shows boundary location nearest Platform Irene.

offshore side (bins 22–39), and the remainder crossed the northern side (6%) or the southern side (1%).

To compare results more directly between years, a histogram of crossings was generated from the 2002 trajectories, using the 1999 coverage boundary. The 1999 coverage boundary was completely contained within the 2002 coverage boundary. With the 2002 trajectories, a peak in the histogram again occurred along the offshore boundary (Fig.4, left-hand scale), this time at bin 12 compared with bin 11 when the 1999 trajectories were used. A second, but much smaller peak occurred along the 50-m isobath at bin 3, consistent with the small peak along the 50-m isobath of Fig. 2B. Table 1 and the cumulative histogram (Fig. 4, right-hand scale) showed that 18% of trajectories crossed the 50-m isobath, 66% crossed the offshore side of the coverage boundary, and the remainder crossed either the northern (7%) or southern (8%) sides.

The time required for trajectories to cross the coverage boundary, defined in our study as the residence time, varied between years and mainly depended on the size of the coverage area. In 1999 the mean and standard deviation for the residence time was 19 ±12 hours, and the maximum was 86 hours (Table 1). In 2002 they were 47 ±34 hours and the maximum was 163 hours. When the 2002 trajectories were computed over the 1999 coverage boundary, residence times were comparable to the 1999 values: 22 ±18 hours and a maximum of 116 hours.

Discussion

Because of limitations in spatial coverage, the HF radar-derived trajectories could not be used to examine the full range of length and time scales over which actual trajectories may extend. We used a trajectory data set resulting from the release of Argos drifters in the region to examine these scales. Drifters were deployed in the Santa Barbara Channel and Santa Maria Basin at irregular intervals from October 1992 through December 1999 as part of a circulation study conducted by the Scripps Institution of Oceanography (SIO; see Dever [1998] and Winant et al. [2003] for a description of the drifter data set). Drifter positions were obtained up to six times per day, typically for 40 days, and had a spatial accuracy of about 1 km. Several trajectories ended earlier when the drifters beached.

No drifters were released at Platform Irene although many approached the platform after release elsewhere (130 drifters were deployed to the north of Platform Irene, and 440 were deployed to the south). To approximate trajectories originating at Platform Irene, all drifters released during all seasons for all years, and approaching within 10 km of the platform, were identified. This distance is a compromise between proximity to the platform and ensemble size; 93 trajectories approached within 10 km of Platform Irene (white circle in Fig. 5 is 10 km in radius and is centered on Platform Irene). Of these, 34 were released north and 59 south of Platform Irene. The ensemble of trajectories beginning

within 10 km of Platform Irene (gray and black dots, Fig. 5) mainly followed the trend of southward advection by the California Current System, although a smaller number extended northward from the platform and a few reached Monterey Bay. Four trajectories entered the Santa Barbara Channel.

A further sorting of the ensemble of 93 trajectories approaching within 10 km of Platform Irene to include only those during 1 May–31 August of all years produced a subset of 21 trajectories (black dots, Fig. 5). Of these, 17 crossed the 2002 coverage boundary: 3 on the 50-m isobath, 12 on the offshore boundary, 2 on the northern boundary, and 0 on the southern boundary. Although the ensemble was small, the fraction of drifters crossing the inshore boundary of the 2002 coverage area (18%) was comparable to the fraction of HF radar-derived trajectories that did so (24%), as shown in Table 1. Most trajectories crossing the offshore boundary continued offshore and southward, consistent with advection by the California Current System. Others crossing the offshore boundary extended north of Platform Irene before turning southward or offshore. The two trajectories crossing the northern boundary remained near shore and crossed the 50-m isobath north of the platform. None of these 17 trajectories entered the Santa Barbara Channel. Except for three drifters that beached, all the drifters remained offshore for the duration of Argos data logging.

Trajectories crossing the 50-m isobath tended to do so north of platform Irene, as shown by most of the computed trajectories and three of the SIO drifters (Figs. 2B and 3B). This movement indicates that transport from the platform to shallow water habitat along the mainland coast mostly occurred during times of northward, or poleward, currents. Poleward flow in the region north of Pt. Conception results from weakening or reversal of the prevailing upwelling favorable winds, the so-called "relaxation" flow state described by Dever (2004), Harms and Winant (1998), and Winant et al. (2003). They also described two other flow states, "upwelling" and "convergent," which produce offshore and equatorward transport near Platform Irene. Together these flow states have a 69% probability of occurring during May–Aug (36% for upwelling and 33% for convergent), whereas the relaxation state has a 23% probability of occurring (Winant et al. [2003], their Table 3). For comparison, 19–30% of trajectories (HF radar-derived plus actual drifters) crossed the inshore and northern boundaries, consistent with the relaxation probability and 70–81% crossed the offshore and southern boundaries, consistent with the upwelling plus convergent probability.

The trajectories can also be used to estimate recruit survival, based on the time required for transport to habitat. Recruit survival is estimated from a simple exponential decay model:

$$P(t) = P_0 e^{-mt}, \quad (3)$$

where m = mortality (0.02 or 0.06/day, Ralston[2]);

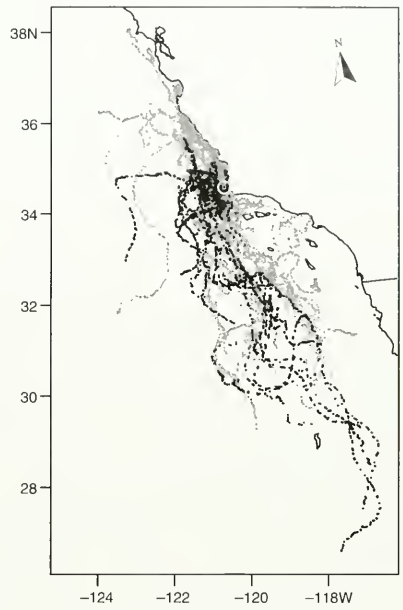

Figure 5

Trajectories of all drifters deployed by the Scripps Institution of Oceanography at various times from October 1992 through December 1999 after passing within 10 km of Platform Irene (gray dots). Also shown are all drifters after passing within 10 km of Platform Irene for only the time period 1 May–31 August for all years (black dots). White circle is centered on Platform Irene and has a radius of 10 km.

P = population at time t; and
P_0 = the initial population.

Here, P_0 represents the population of juvenile bocaccio that recruited at Platform Irene, and survival estimates are used to predict their survival in the absence of the platform. In 1999 and 2002, trajectories to habitat from Platform Irene crossed the 50-m isobath within 19–47 hours (Table 1), indicating a high percentage of survival for bocaccio (96–98%). In contrast, offshore and southward drifter trajectories from the SIO drifter data indicated much lower survival. Pelagic juvenile bocaccio transported by these flows would be carried southward by the California Current and remain far from the mainland and the Northern Channel Islands (Fig. 5)

[2] Ralston, S. 2004. Personal commun. NOAA National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, CA 95060.

for at least 40 days, the nominal time the drifters were tracked. Survival after 40 days along these trajectories ranged from 9 to 45%.

It is possible that juvenile bocaccio spend time away from near surface waters during their planktonic larval phase and therefore their trajectories may depend on deeper currents. Previous observations in the study region show strong correlation between near surface and deeper flows, indicating that inferences from surface trajectories apply to deeper trajectories. Comparing moored current meters at 5 and 45 m depth, Dever (2004), Harms and Winant (1998), and Winant et al. (2003) generally found a high correlation between current directions, and a decreased flow speed at depth. They also found that poleward flow at 45 m occurs during the convergent and relaxation states, and equatorward flow occurs during the upwelling state. Therefore, during relaxation and upwelling states, currents at 45 m likely have similar directions, but lower speeds compared with surface currents. During the convergent state, currents at 45 m are opposite surface currents, indicating that surface currents represent deeper currents only to some shallower depth.

We assumed in this trajectory analysis that juvenile bocaccio effectively behave like passive particles. We made this assumption for two reasons: 1) this assumption allowed us to focus on the lower bound of their range of possible swimming behaviors; and 2) such an assumption also eliminated the need to account for their actual swimming behavior in the open ocean, about which little is known. We do not assume that juvenile bocaccio do not swim; rather, we assume that they swim randomly such that their effective transport is similar to that of passive particles. The other behavioral limit of rapid, consistently directional swimming behavior would likely alter the fraction of bocaccio encountering shallow habitats versus the fraction being advected offshore. Flume experiments with visual cues for directional orientation demonstrate that coral reef fish in the late pelagic stage can swim up to ~100 km in 8 days (Stobutzki and Bellwood, 1997); therefore behavioral modification of trajectories could be very important. Larval and pelagic juvenile fish may possess swimming and sensory abilities to overcome passive drift in currents; however, some kind of external reference is necessary for fish to detect and respond to the direction of a current. In a review of the behavior of larval and juvenile fish in the pelagic environment, Leis and McCormick (2002) pointed out that it is yet to be demonstrated that these early-stage fish in offshore "blue water" can effectively modify current-driven trajectories by orienting to cues from settlement habitat located at a scale greater than several kilometers away. A variety of near-field stimuli, such as light and temperature gradients, sound, and visible prey affect swimming behavior. Clearly more research is needed to evaluate the effects of swimming behavior of temperate reef fishes, such as bocaccio, in order to model their dispersal. We speculate, however, that the assumption of passive dispersal will remain an important lower bound on constraining effects of swimming behavior.

Smoothing and interpolation in the processing of the HF radar velocity data limit the spatial resolution of current fluctuations to scales of ~6 km, the diameter of circles used to compute velocity vectors. Velocity structures smaller than this scale are not resolved but may be important in determining trajectories. For example, Helbig and Pepin (2002) found that errors in modeling the spatial distributions of fish eggs in an embayment increased as spatial resolution of a circulation model decreased. Assuming effects of unresolved velocity structures on smaller scales act as a diffusive process, we speculate that incorporating diffusion would cause the locations of the boundary intersections to spread to adjacent bins. In this case, peaks in the histograms (such as in Figs. 2B, 3B, and 4) would decrease as diffusion spreads boundary intersections to adjacent bins. Velocity statistics at scales of the order of a few km and smaller in our study area, however, are not available for incorporating the effects of diffusion into the trajectories. Results from actual drifters, which do contain velocity structure unresolved by the HF radars, are not very different from HF-radar-derived trajectory results (Table 1), indicating that the effects of unresolved variance are not large. For predicting settlement to habitat, trajectory improvements gained through the incorporation of smaller scale flow features may be offset by assumptions of swimming behavior and habitat location.

Questions and issues have arisen in the decommissioning process about the regional importance of platform fish assemblages (Schroeder and Love, 2004). For example, does removal of a platform impact the bocaccio population? Based on our annual research submersible surveys (detailed in Love et al., 2003) conducted in 1997, 1998, 1999, and 2001, estimates of YOY bocaccio at Platform Irene ranged from 61 (2001) to 41,000 (1999) (Lenarz[3]). YOY bocaccio abundances can be even higher than those observed at Platform Irene. We have recently estimated that, during 2003, Platform Grace, located in the Santa Barbara Channel, harbored over 300,000 YOY bocaccio (Lenarz[3]). Under even the most conservative parameters, this would translate into many thousands of adults (MacCall[4]). In addition, there is evidence that some of the bocaccio that recruit to platforms as YOYs migrate, and thus seed, natural reefs. Fish tagged at Platform A, located off Summerland, CA, in the Santa Barbara Channel, were later recovered over natural reefs over 100 km to the north and south of that platform (Hartmann, 1987). In another study, recruiting bocaccio became resident on a deep-water platform and formed the highest density of adult fish observed in the Southern California Bight

[3] Lenarz, W. 2004. Personal commun. P.O. Box 251, Kentfield, CA 94914-0251.

[4] MacCall, A. 2004. Personal commun. NOAA National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, CA 95060.

(Love et al., 2003). Thus, bocaccio that recruit as YOYs to a platform may benefit natural reefs either through emigration to these reefs or through increased larval production.

Conclusion

Observations of evolving surface current patterns obtained by HF radar are used to estimate dispersal pathways for juvenile bocaccio in the vicinity of Platform Irene, an oil production platform off the central California coast. Results indicate that most of YOY bocaccio settling around Platform Irene would not survive in the absence of the platform. Instead, prevailing currents would likely advect them offshore where they would have a very low probability of survival. Although it is possible that some individuals would encounter acceptable nursery habitat on offshore banks or islands, it is likely that most would perish. Thus, the presence of Platform Irene almost certainly increases the survival of young bocaccio in the Point Conception–Point Arguello region.

These results indicate that knowledge of regional ocean circulation patterns is essential for evaluating the effects of oil production platforms, or other artificial habitats, on dispersal pathways of juvenile fishes. Platform location, local current patterns, and natural habitat distribution determine the balance between settlement at a specific platform and settlement on natural habitat. The approach used in this study, an analysis of trajectories derived from HF radar current measurements, can provide insights into this balance. Additional research on small-scale circulations features unresolved by the radars and on swimming behavior of juvenile rockfishes will sharpen these insights.

Acknowledgments

We thank S. Ralston, NMFS, Santa Cruz, for providing pelagic juvenile bocaccio mortality estimates; W. Lenarz for YOY bocaccio abundance estimates at Platforms Irene and Grace; and A. MacCall, NMFS, Santa Cruz, for projected survival of the YOY bocaccio. We benefited from helpful discussions with Edwin Beckenbach and David Siegel. Drifter data were made available by the Center for Coastal Studies at the Scripps Institution of Oceanography. David Salazar and Chris Gotschalk provided valuable support during field operations. This research was supported by the Minerals Management Service, U.S. Department of the Interior, MMS Agreement 14-35-0001-30758; the California Artificial Reef Enhancement Program; the W.M. Keck Foundation; the Biological Resources Division of the U.S. Geological Survey; the University of California Marine Council; the National Oceanographic and Atmospheric Administration; and PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation, and the David and Lucile Packard Foundation (contribution number 191). Deploying the radars was made possible through cooperative agreements with the California State Parks Channel Coast District, the U.S. Coast Guard, and the U.S. Air Force.

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Abstract—Behavior of young (8–18 mm SL) giant trevally (*Caranx ignobilis*), a large coral-reef–associated predator, was observed in the laboratory and the ocean. Size was a better predictor of swimming speed and endurance than was age. Critical speed increased with size from 12 to 40 cm/s at 2.7 cm/s for each mm increase in size. Mean scaled critical speed was 19 body lengths/s and was not size related. Swimming speed in the ocean was 4 to 20 cm/s (about half of critical speed) and varied among areas, but within each area, it increased at 2 cm/s for each mm increase in size. Swimming endurance in the laboratory increased from 5 to 40 km at 5 km for each mm increase in size. Vertical distribution changed ontogenetically: larvae swam shallower, but more variably, and then deeper with growth. Two-thirds of individuals swam directionally with no ontogenetic increase in orientation precision. Larvae swam offshore off open coasts, but not in a bay. *In situ* observations of *C. ignobilis* feeding, interacting with pelagic animals, and reacting to reefs are reported.

Behavioral ontogeny in larvae and early juveniles of the giant trevally (*Caranx ignobilis*) (Pisces: Carangidae)

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Manuscript submitted 16 December 2004 to the Scientific Editor's Office.

Manuscript approved for publication 27 September 2005 by the Scientific Editor.

Fish. Bull. 104:401–414 (2006).

The giant trevally (known as ulua aukea in Hawaii) (*Caranx ignobilis* (Forsskål)), is the largest species in the commercially important family Carangidae. It has a wide tropical Indo-Pacific distribution ranging from Japan to Australia and from East Africa to the Hawaiian and Marquesas Islands (Randall et al., 1997; Smith-Vaniz, 1999; Hoese et al., in press). Adults of this reef-associated pelagic species may be solitary or form schools on inner reefs, inshore on sand flats, or in reef channels, but primarily on seaward reefs to depths of 80 m (Kuiter, 1993; Myers, 1999; Hoese et al., in press). *Caranx ignobilis* is an important top-level carnivore in reef systems: adults and juveniles feed during the day primarily on demersal and pelagic fishes and to a lesser extent on cephalopods and crustaceans (Blaber et al., 1983; Sudekum et al., 1991; Myers, 1999). Adult coloration varies from silver grey to almost black above and fins are usually dark grey to black, but in small juveniles the body is barred (pale to dark gray) and the anal and caudal fins are yellow (Kuiter, 1993; Randall et al., 1997). *Caranx ignobilis* is important to commercial and recreational fisheries and to aquaculture because of its size (maximum of 1.7 m and 62 kg), abundance, palatability, and reputation as an excellent game fish (Smith-Vaniz, 1999; Yu, 2002). The species can, however, be ciguatoxic (Myers, 1999).

Little is known of the early life history of *C. ignobilis*. Adults, which reach maturity at about 60 cm in length and 3–4 years of age, have been reported to gather on shallow seaward reefs and offshore banks to spawn (von Westernhagen, 1974; Johannes, 1981; Sudekum et al., 1991; Myers, 1999). Neither eggs nor larvae have been described, and nothing is known of the distribution or behavior of the larvae or early juveniles. Juveniles are found in small schools over sandy inshore bottoms (Myers, 1999), but also in turbid estuaries, where they are "uncommon" (Blaber et al., 1983). Juveniles and subadults have wide tolerances for salinity and turbidity (Blaber et al., 1983). In Kaneohe Bay, Hawaii (a coral-reef lagoon with estuarine features), *C. ignobilis* juveniles less than 20 cm (<1 year old) were found on the "murky" lagoon floor (Wetherbee et al., 2004). Juveniles were associated with lagoonal patch reefs when they were between 25 and 40 cm in length, and appar-

ently moved out of the bay when larger than 40 cm. In South African estuaries, individuals larger than 55 cm were absent (Blaber et al., 1983). The high abundance of *C. ignobilis* in the NW islands of Hawaii (Sudekum et al., 1991), where estuaries are absent, shows that presence of juveniles in estuaries is facultative.

Recently, Taiwanese aquaculturists have developed culture methods for *C. ignobilis* (Yu, 2002), and this enabled us to obtain larvae and small juveniles that we used for laboratory and field observations of behavior. Behavior of early-life history stages of marine fishes can strongly influence both the survival and distribution of these small fishes (Leis and McCormick, 2002). Therefore, an understanding of the behavioral capabilities of these early-life history stages is essential to intelligent management, and to comprehend the demographics and ecology of any marine teleost fish.

Aside from field studies of the behavior of wild larvae in vertical distribution (e.g., Ahlstrom, 1959; Olivar and Sabatés, 1997; Flores-Coto, et al., 2001), behavior has been studied in the early-life history stages of only a few carangid fishes. There has been extensive research on cannibalism, aggressive interactions, and schooling behaviour by using reared larvae and juveniles of Japanese amberjack (*Seriola quinqueradiata*) and white trevally (*Pseudocaranx dentex*) in the laboratory (e.g., Masuda and Tsukamoto 1996, 1998, 1999; Sakakura and Tsukamoto 1996, 1999). We report in the present study the first observations of the development of swimming abilities, orientation abilities, and vertical distribution for *C. ignobilis,* using both *in situ* methods (Leis et al., 1996) and laboratory swimming chambers (Fisher et al., 2000). These behaviors are important to dispersal, feeding, predator interactions, and survival generally during the early life history of *C. ignobilis*.

Materials and methods

Larvae and juveniles

Young *C. ignobilis* were obtained from a commercial aquaculture farm near Kaohsiung, Taiwan. They were identified as *C. ignobilis* by the farmer with reference to photographs, and the identification was subsequently confirmed by examination of preserved specimens. *Caranx ignobilis* eggs from an induced spawn were placed in a large outdoor earth pond (approximately 20×20×1m), and thus hatched under "natural" conditions. Larvae were provided with a "natural" food source (phytoplankton and zooplankton that were resident in the pond). Surface water temperature in the outdoor pond was 32°C when the larvae were collected in May 2004. Fish were obtained on two occasions at the same pond from a single cohort and from an unknown number of females; the first collection was at 20 days after hatching (dah) and the second at 24 dah.

The young fish were placed in oxygenated plastic bags in an insulated box and transported to the laboratory at the National Museum of Marine Biology and Aquarium (NMMBA), Kenting, Taiwan, about 1 hour by road. In the laboratory the larvae were acclimated in a 40-liter aquarium filled with water from the seawater system at NMMBA. Each aquarium was fitted with an aerator, and kept ca 25°C. Twice daily, the larvae were fed with live, newly hatched brine shrimp (*Artemia*) nauplii and 50% of the total volume of water exchanged with fresh seawater. The aquaria were cleaned daily by suctioning debris off the bottom.

Reported sizes of larvae are given in standard length (SL, in mm). Ages are reported as days after hatching (dah) and are based on the age reported by the aquaculturist when the larvae were obtained. The nomenclature for early life history stages of fishes is complex; there are many different systems of terminology and no consensus on which is the most appropriate. Depending on the nomenclature used, the *C. ignobilis* individuals we studied (Fig. 1) would be considered larvae, or juveniles, or as a mixture of both. In our *C. ignobilis*, all fin-rays were present in the smallest specimens (8 mm), and scales were present from about 14 mm, yet the preopercular spines that characterizes most carangid larvae (Leis and Carson-Ewart, 2004) were still present at 19 mm. Unlike the pelagic stages of demersal fishes, *C. ignobilis* does not undergo a clear ecological transition from pelagic to demersal habitat upon which one might base life history stages. We do not attempt to distinguish between larvae and juveniles, and to avoid awkward phrasing and for simplicity, we refer to the young fish that we studied as larvae on the basis that the largest individuals retained some head spines. We acknowledge that in some taxonomic systems they may be referred by other terms.

Laboratory observations

Multilane swimming chambers were used to measure swimming abilities (Stobutzki and Bellwood, 1994). One chamber was used to measure critical speed and a second identical chamber was used for measurements of endurance (Fisher et al., 2000). Both chambers were made of clear plexiglass and had 6 lane-ways, each 30 mm wide, 50 mm high, and 180 mm long. A black line across the lid of the chamber provided the larvae with a point of reference for orientation. Aside from the fine mesh (0.5-mm) ends, the chamber design was identical to that of Stobutzki and Bellwood (1994, 1997).

Even distribution of flow was achieved by a T-piece diffuser in the header portion of the chamber. Turbulence in the chamber was minimized by a 40-mm-long section of flow straighteners at the start of each lane. These straighteners also minimized possible boundary layers. Previous measurements have shown that water velocity in the 5 mm area closest to the wall was not significantly different from that in the center of the chamber (Stobutzki and Bellwood, 1997; Stobutzki, 1998; Fisher et al., 2000). Water flow speed was controlled by turning a calibrated ball valve. Flow rates were calibrated by recording the time taken for water

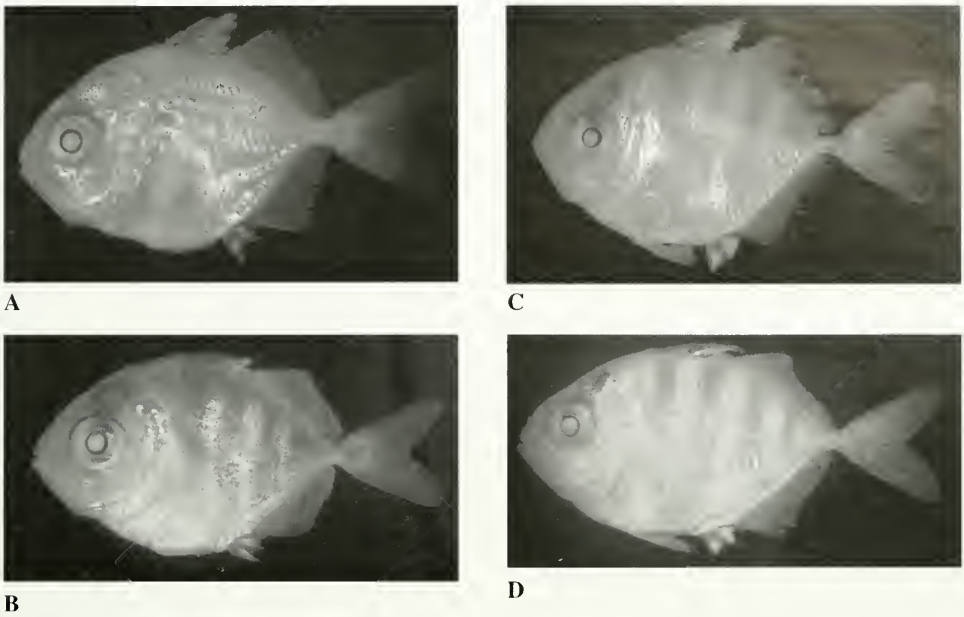

Figure 1

Preserved larvae of giant trevally (*Caranx ignobilis*) representing the range of sizes and developmental stages included in the present study. Preopercular spination was present in all specimens. The smallest specimen had a few scutes on the peduncle, the 14.5-mm specimen had scales forming elsewhere, and the largest specimen was largely scaled. Sizes are SL (Australian Museum catalogue numbers are provided). (**A**) 9.6 mm (I.43435-004); (**B**) 11.7 mm (I.43435-003); (**C**) 14.5 mm (I. 43435-004); (**D**) 18.5 mm (I.43435-002).

flowing over the outlet weir to fill a container of known volume, divided by the cross-sectional area of the chamber. The average of five calibrations was used as the flow speed for a given valve angle. The chambers were calibrated each time they were set up. Flow speeds in excess of 50 cm/s could be achieved with this system. The chambers were plumbed into the seawater system of the NMMBA aquaria and laboratory, which provided a continual flow of "fresh" seawater.

Before measurements of swimming speed and endurance were recorded, the larvae were acclimated to any differences in water quality between the holding tank and swimming chamber by gradual addition of seawater from the swimming chamber system. Larvae were placed in a chamber lane and allowed to acclimate for 5 minutes at 1 cm/s. Any larva showing signs of stress during the acclimation period was removed from the experiment and replaced with another individual. Water temperature in the swimming chamber ranged from 27° to 29°C. Two swimming parameters were measured: critical speed (U_{crit}), which measures maximum swimming speed over periods of minutes, and endurance, which measures how long larvae can swim without food or rest.

For U_{crit} tests, starting at 1.5 cm/s flow speed was increased by approximately 2 cm/s every 5 minutes until the larvae were unable to swim against the flow. The elapsed time when each larva drifted to the downstream mesh was recorded. Critical speed (U_{crit}) of larvae was calculated with the equation of Brett (1964):

$$U_{crit} = U + (t/t_i \times U_i),$$

where U = penultimate speed;
U_i = speed increment (ca. 2 cm/s in the present study);
t = time swum in the final speed increment; and
t_i = the time interval for each velocity increment (5 min).

The total time for a critical speed measurement was proportional to the U_{crit} achieved, and varied from 15

Table 1

Location-specific relationships between *in situ* speed (cm/s) and size (mm SL) in *Caranx ignobilis* larvae. NA=not applicable.

Location	n	Regression	r^2	P
Wan Li Tong	7	$Spd = 1.69SL - 6.2$	0.83	<0.002
Her Chen	3	$Spd = 2.55SL - 12.2$	0.97	0.11
Nan Wan Bay South	2	$Spd = 0.12SL + 4.9$	NA	NA
Nan Wan Bay North	6	$Spd = 2.05SL - 17.9$	0.72	0.03

minutes for the slowest individual to 82 minutes for the fastest. Given the endurance of which these larvae are capable (see "Results" section), it is unlikely that the larvae would have become fatigued over such time intervals.

For endurance tests, a constant speed of 10 cm/s was used. Larvae were swum until they fatigued, which was defined as the time when a larva could no longer hold its position against the current and drifted onto the downstream mesh. During daylight hours, larvae were observed regularly and the exact time of fatigue (=swimming duration) was recorded. If a larva fatigued when it was not being observed, the time at fatigue was estimated as the midpoint between the time when the larva was last seen swimming and the time when it was found no longer swimming. Chambers were set up under cover so that they were shaded throughout the day, and a fluorescent light was used for illumination at night. The actual endurance measurements of time swum were converted to distance swum, by using the flow speed data, and were reported as kilometres swum.

Fatigued larvae from both experiments were removed from the chamber, euthanized and fixed in Bouin's solution for one hour, then placed in 70% alcohol and stored. All preserved larvae were later examined under a dissection microscope to determine standard length (SL) and state of notochord flexion. Total lateral area (TA) and propulsive area (PA) of larvae (Fisher et al., 2000) were measured by using Scion Image for Windows (Beta 4.02, Scion Corporation, Frederick, MD). PA is TA minus the head and gut.

In situ observations

Four sites were used for *in situ* observations of *C. ignobilis* in the South China Sea, at the southern tip of Taiwan (ca. 22°N, 121°E). Two study sites were used in Nan Wan Bay (21 May 2004) where the depth range was 14–23 m and another two were used on the west coast just off the peninsula that delineates the west side of Nan Wan Bay in the vicinity of Wan Li Tong and Her Chen (14 May 2004) at a depth range of 17–31 m (Table 1). At each site, observations were made at least 50 m offshore, and all observations were conducted in the morning.

Larvae were transported from the laboratory to the release sites in covered buckets fitted with a battery-operated aerator. Ambient seawater was gradually added to the buckets to allow the larvae to acclimatize to the surrounding water conditions. Then, 50% of the water in the bucket was exchanged for "fresh" seawater every hour. The behavior of the larvae was observed following the procedures of Leis et al. (1996) and Leis and Carson-Ewart (1997, 1998). Two scuba divers descended to a depth of 5 m where the observer diver released a larva from a small container. Once the larva chose its initial trajectory, the two divers followed. The observer diver's sole job was to follow the larva while the second diver, following the observer, recorded data. The direction the observer diver was facing when he or she released the larva was chosen at random. Each larva was used only once and, where possible, was recaptured at the end of the observation period and preserved. The size of each larva was estimated, with the aid of a ruler, before release. For recaptured larvae, the estimated and actual sizes were regressed, and this relationship was used to calculate the actual size of the five individuals that were not recaptured of the 24 released. Water column depth was measured by the depth sounder on the support boat at the start of each larval release.

Swimming speed, depth, and swimming direction were measured *in situ*. We attempted to observe each larva for 10 minutes, taking measurements of swimming direction and depth, using a dive compass and computer, respectively, every 30 seconds. Speed was calculated from distance traveled as measured by a calibrated flowmeter over the full period of observation (Leis and Carson-Ewart, 1997). Larvae were not followed deeper than 15–18 m on some dives for safety reasons; therefore observations on some individuals were curtailed. Twenty-four larvae were observed, and observations on 18 of the larvae lasted the full 10 minutes. Five larvae swam monotonically downward to below our safety depth from 3 to 6 minutes, whereas one initially ascended, before descending after 5 minutes and exceeding the safety depth after 8 minutes.

Data analysis

To determine the best predictor of performance, values of critical swimming speed and endurance were regressed against SL, TA, and PA by using linear, logarithmic, power, and exponential models. The model with the greatest r^2 (coefficient of determination) was used as the best description.

All bearings are given as degrees magnetic. Cardinal directions are not abbreviated, but other directions are abbreviated (e.g., SE for southeast). From these bearings and the flowmeter data, we estimated swimming direction and speed in relation to the water (not the bottom).

Circular statistical procedures followed Batschelet (1981) and Zar (1996). Mean vector length (r), is a measure of angular dispersion ranging from 0 (maximum dispersion) to 1 (lack of dispersion). The Rayleigh test was used for single-sample hypotheses about directional swimming. Watson-Williams test was used for hypotheses about directional swimming involving more than one sample. Most of the circular statistical procedures were performed with Oriana software (vers. 2, Kovach Computing Services, Pentraeth, Wales, UK). For all statistical tests, we report actual P values whenever possible, but consider $P<0.05$ to constitute a "significant" result.

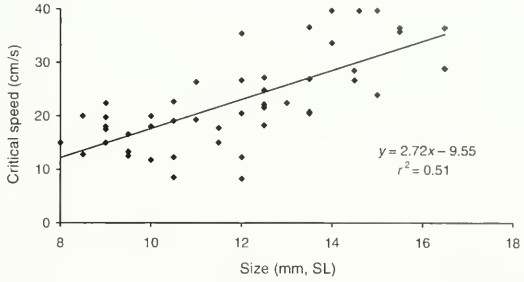

Figure 2

Critical speed of giant trevally (*Caranx ignobilis*) larvae of different sizes. At any size, variation in swimming speed was large.

Results

Larvae used in the critical speed trials were 21–30 days old, and ranged from 8.0 to 16.5 mm SL. Larvae up to 18 mm were used in the *in situ* observations. All fins were formed in the smallest individual and over the size range studied, the larvae were very deep bodied, primarily silver, and usually had six dark vertical bars laterally. Although the specimens used on any day did not constitute a random sample of the available sizes, they could be used to obtain a rough estimate of the growth rate over the experimental period. The range of size-at-age on any day was as much as 6.5 mm. Average growth over this period was 0.36 mm/d, and the slope of the size versus age line was significantly different from zero, but the relationship between size and age was weak (size=0.36 age + 2.87, $P<0.001$, $r^2=0.28$). Total lateral area increased approximately as the square of SL ($TA=0.51SL^{2.01}$, $r^2=0.93$), whereas propulsive area increased at a lower rate ($PA=0.34SL^{1.96}$, $r^2=0.94$).

Critical speed

Critical speed was measured in 54 individuals in eight batches of six over 10 days. Critical speed increased with size from about 12 cm/s in the smallest individuals (ca. 8 mm) to about 40 cm/s in the largest (16.5 mm, Fig. 2). For SL, a linear model provided the best fit for this relationship ($U_{crit}= 2.72SL-9.55$, $P<0.001$, $r^2=0.51$, $n=54$), but the difference between the linear model and the others was small (r^2 for the other models ranged from 0.43 to 0.49). Both TA and PA gave somewhat better fits than SL ($U_{crit}= 0.39TA + 5.25$, $r^2=0.58$; $U_{crit}= 0.22PA +5.73$, $r^2=0.55$). Size was a much better predictor of critical speed than was age ($U_{crit}=0.90age-0.22$, $P<0.01$, $r^2=0.13$, $n=54$).

The fastest individual within each 1-mm increment of size was considered the best performer, and these constituted 16.6% of all larvae. These nine best performing larvae swam at 20 to 40 cm/s. The nine best performing larvae had the same increase in performance with size (2.7 cm/s per each mm of growth) as the "all-individuals" line, but were 8 cm/s faster at all sizes ($U_{crit}=2.69SL-1.46$, $P<0.001$, $r^2=0.76$). Therefore, both average performers and "best performers" increased speed at 2.7 cm/s per each mm of growh in SL.

Scaled speed in terms of body lengths per second did not increase significantly with size ($P=0.07$, $r^2=0.06$), and the overall mean (±standard error) was 19 ±0.7 BL/s. The fastest 10% of individuals swam at a mean U_{crit} of 28.2 ±0.6 BL/s.

In situ speed

In situ speed was measured in 24 individuals ranging in size from 8.5 to 18 mm SL. Some individuals stopped and hovered at times during the observation period, but these pauses in swimming were incorporated into the speeds measured over the observation period. Observations were made a week apart when the larvae were 24 and 31 days old, respectively, and at a total of four locations that differed in depth, exposure, and bottom type. Observed *in situ* speeds ranged from 3 to 19 cm/s. The *in situ* speeds were less than the critical speed measurements (see below). Mean scaled *in situ* speed was 9.5 ±0.9 BL/s.

Overall, there was no significant increase in speed with size ($P=0.89$, $r^2=0.001$, $n=24$), but it was obvious that the larvae behaved differently in the different locations; therefore we examined the data for each location separately. Further, we eliminated observations on one larva that simply drifted without swimming and on four individuals that quickly swam to depths greater than 18 m and thus provided less than 5 minutes of observations, because short measurements of speed taken at steep angles of descent can be inaccurate. The *in situ* speed data on the 19 remaining individuals were used.

For each location, *in situ* speed increased with size, as expected, except, perhaps for the largest individual (Table 1, Fig. 3). For the three locations with three or more observations, *in situ* speed increased at 1.7–2.6 cm/s per each mm of growth depending on location (Table 1), and the 95% confidence interval for the three slopes overlapped broadly. However, because the height of the speed versus size lines varied (*y* intercept ranged from −6 to −18), the actual speed at any size differed among locations by as much as 10 cm/s. For the *in situ* speed data, PA provided fits with r^2 values that were very similar to those of SL. The r^2 for PA was 0.07 higher than that for SL for Nan Wan Bay North, equal for Her Chen, and 0.15 lower for Wan Li Tong.

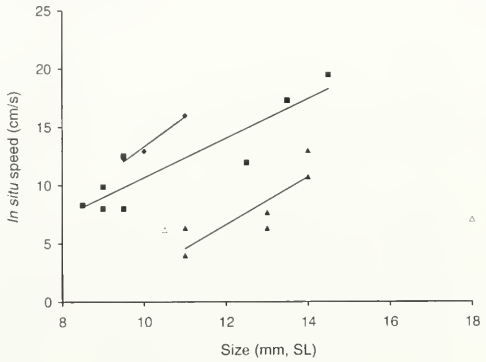

Figure 3

In situ speeds of giant trevally (*Caranx ignobilis*) larvae and juveniles of different sizes at different locations. Locations of observations were ■ Wan Li Tong, 14 May 2004; ♦ Her Chen, 14 May 2004; ▲ Nan Wan Bay North, 24 May 2004; ▲ Nan Wan Bay South, 24 May 2004. See Table 1 for details of best-fitted regression lines for each area. No line was fitted to the two points from Nan Wan Bay South.

Table 2

Comparison of two measures of size-specific speed (cm/s) in *Caranx ignobilis* larvae. Dashes indicate that no data were available.

Size interval (mm, SL)	Mean *in situ* speed (*n*)	Mean U_{crit} (*n*)	Ratio: *in situ*/U_{crit}
8.1–9.0	8.7 (3)	17.5 (3)	0.50
9.1–10.0	11.4 (4)	15.3 (12)	0.75
10.1–11.0	8.1 (4)	18.0 (6)	0.45
11.1–12.0	– (0)	20.2 (9)	—
12.1–13.0	8.6 (3)	24.5 (9)	0.35
13.1–14.0	13.7 (3)	30.7 (7)	0.45
14.1–15.0	19.5 (1)	29.7 (4)	0.66
15.1–16.0	– (0)	36.1 (2)	—
16.1–17.0	– (0)	32.7 (2)	—
17.1–18.0	7.0(1)	– (0)	—
Mean ±SE			0.52 ±0.15

Comparison between critical speed and *in situ* speed

For each 1-mm (SL) increment in size, we calculated a mean speed for both critical speed (54 individuals) and *in situ* speed (19 individuals). These size-specific speeds are summarized in Table 2 (both measurements were not available for every size increment). The ratio of the two size-specific measures (*in situ*/U_{crit}) ranged from 0.35 to 0.75, and had a mean value of 0.52 ±0.15. The size-specific speed measures were not significantly correlated (*in situ*=0.45U_{crit}+1.45, r^2=0.47, P=0.13, n=6). Scaled *in situ* speed (BL/s) was one-half scaled U_{crit}.

Endurance

Endurance data were available for 12 individuals ranging in size from 9 to 14 mm SL, and for two ages (21 and 24 days at the start of the endurance run) measured in two batches of six. The range in fish swimming times was 12.6 to 105 hours. Swimming endurance increased with size from about 5 km in the smallest individuals to about 40 km in the largest (Fig. 4). Again, a linear model provided the best fit for this relationship (*End.*=5.2*SL*−41.5, P<0.001, r^2=0.80, n=12), and the difference between the linear model and the others was small (r^2 for the other models ranged from 0.73 to 0.79). In contrast to critical speed, the fit of the relationship between size and performance was not improved by using TA or PA instead of SL (r^2=0.57 and 0.62, respectively). Endurance also increased with age, but endurance data were available only for larvae of two ages (21 and 24 days). Size was a better predictor of performance than was age (*End.*= 6.6*age*−128, P=0.001, r^2=0.66, n=12).

Vertical distribution

There was not a significant overall relationship between mean swimming depth and size (P=0.29, r^2=0.05). In spite of this, larvae of different sizes differed in their depth selection behavior. The smallest larvae (8–10 and 10–12 mm) swam primarily between 4 and 10–12 m (Fig. 5, A and B). One larva of each of these smallest size groups did, however, swim deep monotonically. If one ignore these two deep-swimming larvae, both smallest size groups reached an overall mean depth of about 9 m

at about 5 minutes. The smaller (8–10 mm) larvae then stayed at about 9 m, whereas the larger (10–12 mm) larvae gradually ascended, reaching a mean depth of about 6 m by the end of the 10-min observation period. In contrast, larvae of 12–14 mm were more varied in their depth ranges, some reaching the surface, whereas others remained within 2–3 m of the release depth (Fig. 5C). Larvae of 12–14 mm had no overall temporal trend in depth and maintained a mean depth of about 5–6 m throughout the study period. Several of the larvae of this group did oscillate over a depth range of several m during the 10-min observation period. The largest larvae (14–18 mm) had more varied vertical-distribution ranges, leading to high amplitudes (Fig. 5D). Three of the five largest larvae swam deep monotonically and the other two oscillated—one reaching the surface after an initial descent, whereas the other reached our lower dive limit (16 m), but only after first ascending above the release depth for the first 5 minutes.

We found a weak relationship between depth amplitude (difference between deepest and shallowest observations) and size ($amp.=0.44SL + 1.7$, $P=0.03$, $r^2=0.21$, $n=24$); larger individuals swam over a greater range of depths owing to the tendency of larger larvae to either oscillate or to swim deep monotonically. Water column depth did not influence either mean swimming depth ($P=0.11$, $r^2=0.11$) or amplitude ($P=0.06$, $r^2=0.15$).

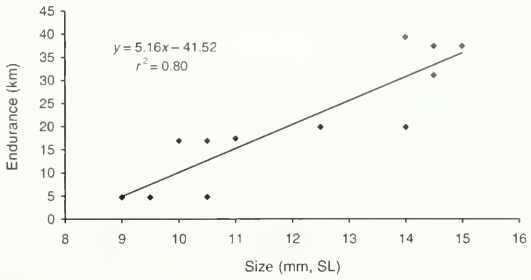

Figure 4

Endurance swimming of giant trevally (*Caranx ignobilis*) larvae of different sizes.

Table 3

Directionality of *in situ* swimming for *Caranx ignobilis* of different sizes. Only values from directional individuals are included for r (the length of the mean vector, which ranges from 0 to 1): the higher r, the more directional was the trajectory.

Size interval (mm SL)	*n*	*n* directional (Rayleigh test, $P<0.05$)	Range of r	Mean r
8–10	8	6	0.41–0.86	0.73
10–12	5	2	0.60–0.90	0.75
12–14	6	4	0.60–0.83	0.72
14–18	5	4	0.45–0.92	0.74

Orientation

Sixteen of the 24 larvae observed *in situ* had directional trajectories ($P<0.05$, Rayleigh test, Table 3). Figure 6 represents the direction frequency distribution of a *C. ignobilis* larva with average directionality. The remaining analyses included only the 16 individuals for which directional trajectories were found (termed "directional larvae" or "directional individuals" for the sake of brevity), but the same result was obtained when all 24 individuals were included. If all locations were considered together, the mean swimming directions of these 16 individuals had no overall directionality ($P>0.20$, Rayleigh test). In contrast, there was significant overall directionality off the west coast (Fig. 7A) where the larvae swam, on average, offshore or toward the west (269°, Rayleigh test, $P=0.024$). There was no indication of any overall directionality in mean swimming direction in Nan Wan Bay (Fig. 7B) (mean direction, 145°, $P=0.58$, Rayleigh test). Overall swimming direction, however, differed significantly between the west coast and Nan Wan Bay (Watson-Williams test, $P=0.028$).

We found only a limited indication that the directionality of the larvae changed with size (Table 3). There was no ontogenetic increase in precision of directionality (measured as r, the length of the mean vector) ($r^2=0.05$, $P>0.10$). Similarly, although the mean size of the eight nondirectional larvae was 11.6 mm, and that of the 16 directional larvae was 12.2 mm, this difference was not significant (*t*-test, $P=0.22$). In terms of overall orientation, larvae observed off the west coast were smaller by about 4 mm (*t*-test, $P=0.002$) and were studied a week earlier than those studied in Nan Wan Bay; therefore it is possible that the difference in overall swimming direction between locations was due to temporal or ontogenetic factors rather than to spatial factors. At the west coast location, the overall mean direction of the five small (8–9.5 mm) directional larvae was the same (268°) as the overall mean direction of the 4 large (10–14.5 mm) directional larvae, indicating there was no ontogenetic change in directionality.

Finally, within trajectories, there was no increase in directionality with time. The r value for the first half of the trajectories was not significantly different from the r value for the second half of the trajectory (Wilcoxon signed-rank test, $P>0.2$). Nor was there any indication that larger larvae had a greater difference in r between the first and second halves of their trajectories than did smaller larvae ($r^2=0.02$, $P>>0.20$).

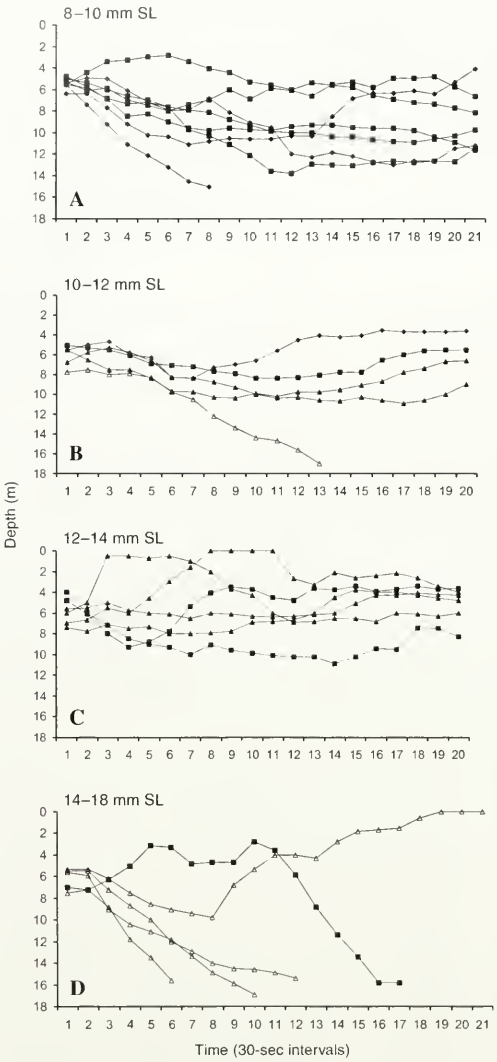

Figure 5

In situ vertical distribution trajectories for giant trevally (*Caranx ignobilis*) larvae and juveniles of four size groups. Locations of observations were ■ Wan Li Tong, 14 May 2004; ♦ Her Chen, 14 May 2004; ▲ Nan Wan Bay North, 24 May 2004; ▲ Nan Wan Bay South, 24 May 2004. (**A**) 8–10 mm SL larvae; (**B**) 10–12 mm SL larvae; (**C**)12–14 mm SL larvae; (**D**) 14–18 mm SL larvae.

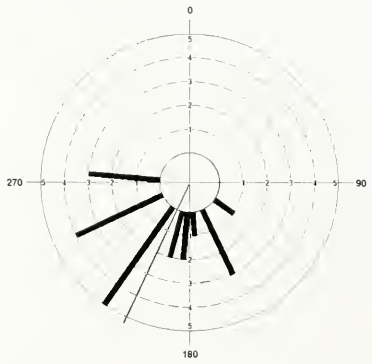

Figure 6

Frequency distribution of *in situ* swimming directions based on bearings taken every 30 seconds for an 18-mm-SL giant trevally (*Caranx ignobilis*,) at Nan Wan Bay South. Bearings are grouped into 10° intervals. The radius that penetrates the outer circle (thin line) is the mean direction. This significantly directional distribution (Rayleigh test, P=0.000001) has an r (length of the mean vector) of 0.76, which is close to the overall mean for the 16 directional individuals (Table 3). The numbers on dashed lines represent the number of times that bearing was recorded for a larva.

Other behaviors

Unplanned observations were made of feeding, interactions with other pelagic animals, and reactions with the bottom. At least nine of the 24 larvae were seen feeding, grabbing at, and apparently eating small zooplankton while swimming. One 12-mm larva encountered a large (ca. 30–40 cm) *Naso* sp. in open water and changed direction by 140° over the following minute. An 11-mm *C. ignobilis* encountered a jellyfish and briefly (<30 s) hovered under it. Five individuals (9–13.5 mm SL) came into visual contact with relatively high-relief coral reefs (at least the divers could clearly see the reefs) at Wan Li Tong and Her Chen. The larvae showed no particular interest in the reefs; two ascended slightly (0.5–1 m), two maintained a distance of 3–4 m from the reef surface as they swam over it, and one turned offshore. One 12.5-mm larva passed through a strong thermocline at 8 m that was very noticeable to the divers without slowing or giving any indication that the temperature change was sensed.

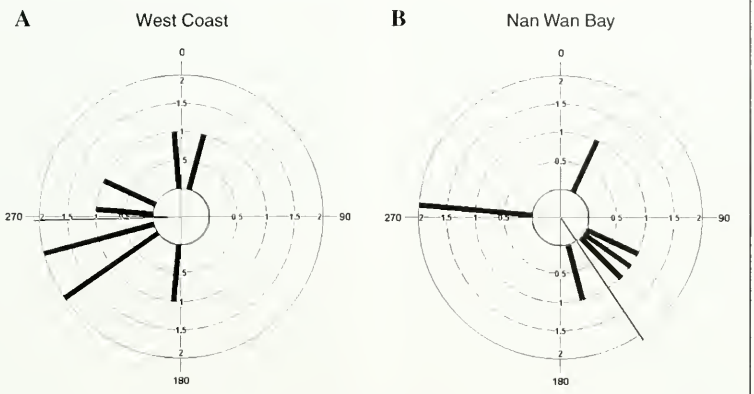

Figure 7

Frequency distributions of mean *in situ* swimming directions for giant trevally (*Caranx ignobilis*) larvae at two locations. Thick lines represent mean values for individuals, and the radius (thin line) that penetrates the outer circle represents the overall mean. The numbers on dashed lines represent the number of times that bearing was recorded for a larva. (**A**) West coast off Wan Li Tong and Her Chen, where larvae swam offshore: overall mean=268°, r=0.59, P=0.04. (**B**) Nan Wan Bay, where larvae had no overall swimming direction: overall mean=146°, r=0.29, P=0.58. "r" is the length of the mean vector, P is for the Rayleigh test.

Discussion

Previous studies of the behavior of larval carangids have focused primarily on their vertical distribution in the ocean and have been based on plankton net samples and on observations of the development of schooling-related behavior in the laboratory (see references at the beginning of this article). There have been no previous studies on the ontogeny of orientation or of vertical distribution determined from *in situ* observations, and only one article has considered the development of swimming abilities of carangid larvae.

Growth rates in *C. ignobilis* larvae of 0.36 mm/d in the laboratory and ca. 0.3–0.8 mm/d at the aquaculture farm at Kaohsiung, where we obtained larvae for our experiment, were comparable to the few reported field growth rates for larvae of other carangids. Small (<5 mm SL) larvae of Atlantic bumper (*Chloroscombrus chrysurus*) grew at 0.3–0.4 mm/d in the Gulf of Mexico (Leffler and Shaw, 1992), and larvae of two species of *Trachurus* grew at 0.2–0.7 mm/d (Hewett et al., 1985; Jordan, 1994). The *C. chrysurus* larvae were found at 26–30°C, whereas the two *Trachurus* spp. were living at about 15°C. In *T. declivis* (greenback horse mackerel), 8-mm larvae were about 17 days old and 12-mm larvae were about 22 days old (Jordan, 1994). In *T. symmetricus* (Pacific jack mackerel), a 10-mm larva was 40 days old and a 20-mm larva was about 57 days old (Hewitt, 1981). Growth rates for *C. ignobilis* in culture or in the laboratory are unlikely to be relevant to field situations, and the available field measurements of other species are either for much smaller larvae or for individuals in much cooler water and are unlikely to be applicable to *C. ignobilis*. Therefore, it is not possible to relate the size-based performance measures reported in our study to ages of larvae in the field. Further, for the laboratory-reared larvae that we used, size was a much better predictor of performance than was age, as is generally found to be the case (e.g., Fuiman and Higgs, 1997; Clark et al., 2005). We found that using PA instead of SL as a measure of size resulted in little or no improvement in the proportion of the variation in swimming performance that was explained by the linear relationships developed in our study. Other studies have had mixed results in this regard (Fisher et al., 2000; Clark et al., 2005).

Swimming speed of *C. ignobilis* increased rapidly with growth for both critical speed and *in situ* speed, although the rate of increase was greater for critical speed. Both in terms of actual speeds and rate of increase with growth, critical speeds of *C. ignobilis* are within the range of reported values for larvae of other warm water marine perciform fishes (Fisher et al., 2000; Clark et al., 2005). For larvae of benthic fishes about to settle (ca. 8–12 mm SL), pomacentrids have higher U_{crit} values than *C. ignobilis*, whereas apogonids, percichthyids, sciaenids, and sparids have similar U_{crit} values. *Seriola quinqueradiata* is the only other caran-

gid for which we could find information on ontogeny of swimming abilities (Sakakura and Tsukamoto, 1999), although the method of measuring swimming performance (so-called "routine speed") differed from those used in our study. Reared *S. quinqueradiata* larvae and juveniles of 5–40 mm TL were filmed swimming in small (30-cm diameter, 7-cm deep) laboratory tanks lacking currents and the speed was measured over 3-min intervals. Speed of *S. quinqueradiata* increased at about 0.4 cm/s per each mm of growth until about 10 mm TL, after which speed remained steady at about 2–2.5 cm/s. This is much slower, both in terms of rate of increase and absolute speed, than was found for either measure of swimming speed in *C. ignobilis*. Possibly, the slow speeds for *S. quinqueradiata* were due to the small containers in which the fish were confined and which lacked currents, as has been found for other species (Theilacker and Dorsey, 1980).

Although we did not study larvae smaller than 8 mm SL, it is safe to assume that smaller larvae have poorer swimming abilities. Previous investigations of swimming ontogeny have revealed that critical speed increases steadily with size (Fisher et al., 2000; Clark et al., 2005), as we did in our study; therefore it seems likely that a reasonable estimate of performance of smaller larvae can be obtained by extrapolating the linear relationship in Figure 2. Thus, a larva of 5 mm (about the size when the caudal fin is formed in carangids; Leis and Carson-Ewart, 2004) would be expected to have critical speeds of about 4–5 cm/s. We found that critical speeds for *C. ignobilis* were about twice *in situ* speeds, and similar relationships have been found for larvae of other species at other sizes (Fisher and Wilson, 2004; Leis and Fisher, in press). Therefore, a 5-mm *C. ignobilis* would be expected to be able to swim at about 2 cm/s (=72 m/h) in the ocean. This speed would have limited effectiveness for directly influencing horizontal position, but would be sufficient to determine vertical distribution at scales over which fish larvae are known to migrate vertically.

To put these swimming performances into an ecological context requires knowledge of ambient currents in the area of interest. If it is assumed that effective swimmers (those with swimming speed equal to or greater than average current speed [Leis and Stobutzki, 1999]) have the ability to control their dispersal by horizontal swimming, then the size at which larvae become effective swimmers is of interest to dispersal modelers. For example, at Lizard Island on the Great Barrier Reef, average current speeds are 10–15 cm/s (Frith et al., 1986). At Lizard Island, average performing *C. ignobilis* would become effective swimmers at about 7–9 mm SL on the basis of critical speed, and at about 11–14 mm based on *in situ* speed which is about half of critical speed (assuming the relationship between *in situ* and critical speeds found in the present study). The best performers would be able to reach these mean Lizard Island current speeds at about 4–6 mm SL, if based on critical speed (assuming the relationship in Fig. 2 applies to smaller larvae), and at 8–12 mm if based on *in situ* speed. Larvae that are too small to be effective swimmers may still readily influence their dispersal by other means, particularly by vertical swimming where current velocity is not uniform with depth (Sponaugle et al., 2002; Paris and Cowen, 2004). Speeds of only 1 cm/s (36 m/h) are sufficient for vertical migration, and this could be achieved by very small larvae. Indeed, vertical movements by small carangid larvae are well documented in studies where plankton nets were used (e.g., Ahlstrom, 1959; Olivar and Sabatés, 1997; Flores-Coto, et al., 2001).

In situ speeds of *C. ignobilis* are within the range of those reported for other perciform species, although most of the available values are for settlement-stage larvae of demersal reef fishes (Trnski, 2002; Leis and Fisher, in press). Further, the rate of increase in speed at 1.6–2.6 cm/s per each mm of growth is similar to that found in the three other perciform species for which there are data (0.3–2.0 cm/s per each mm of growth; Leis et al., 2006). Differences in swimming speed among areas has been reported in a variety of reef fish larvae (Leis and McCormick, 2002); therefore finding a difference for *C. ignobilis* was not unexpected. This variation in behavior among areas and the fact that the rate of increase in speed with growth in the field was less than the increase of U_{crit} in the laboratory clearly demonstrates the complexities of applying laboratory measures to the field, and how behavior in the field can vary with location and situation. The cause for differences in behavior among locations was not clear in our study, but it is only through *in situ* observations that such differences can be discovered.

The approximately linear increase in swimming speed with growth found in *C. ignobilis* was similar to that reported in other species (Fisher et al., 2000; Clark et al., 2005). The ontogeny of endurance in *C. ignobilis* was also linear, in contrast to that of some other species, which are reported to have a strongly concave curvilinear increase in endurance with growth (Fisher et al., 2000; Clark et al., 2005). Perhaps this linearity was the result of studying *C. ignobilis* larger than 8 mm. In other species, preflexion and early postflexion larvae (which we did not study) have very low endurance, but endurance increases rapidly with growth in postflexion larvae.

All our speed measurements were made over periods of 10 minutes or less, but endurance measurements showed that speeds of 10 cm/s can be maintained from several to many hours, enabling distances of up to 40 km to be traversed. The ecological relevance of laboratory measurements of swimming endurance is difficult to assess because, on one hand, these are forced measures of performance, and it is unlikely that larval fishes would swim to exhaustion. On the other hand, endurance measurements are made without rest or food, and are therefore conservative because larvae of other species of the size studied in the present study can swim at least three times farther when fed (Fisher and Bellwood, 2001; Leis and Clark, 2005). In any case, it is clear that *C. ignobilis* larvae can swim for extended

periods at speeds that would make them effective swimmers in many situations. According to the relationship in Figure 4, *C. ignobilis* larvae of about 9 mm could swim without food or rest for about 13 hours (5 km at 10 cm/s) at a speed that is within their observed capabilities *in situ*: this ability increases markedly with growth. Clearly, *C. ignobilis* larvae from a size of 1 cm or less are capable of maintaining speeds of similar magnitude to mean ambient currents for periods of time long enough to strongly influence their dispersal.

Knowledge of vertical distribution of fishes is important because many things vary vertically in the ocean, including current velocity, food concentrations, and predators, all of which can strongly influence survival and dispersal. For these vertically varying factors, the conditions that larval and small juvenile fishes actually encounter are fully under their control because swimming abilities and sensory abilities capable of determining vertical position in the water column develop at a very small size. The *C. ignobilis* we observed in the ocean had considerable control over their vertical distribution, and the depths selected changed with size. Masuda and Tsukamoto (1996) noted ontogenetic changes in preferred light intensity in larvae of *P. dentex*, and it is possible that such changes influence the selection of depth in larval *C. ignobilis*. Two notes of caution are necessary in interpreting the depth-selection behavior and ontogenetic changes in this behavior. The largest larvae were primarily observed at one site, and, it is possible that vertical-distribution behavior varies among areas (Leis, 2004). Secondly, the largest larvae tended to swim to below our safety depth and we therefore do not know if they continued to descend, if they subsequently ascended (in accord with the oscillatory behavior observed in a number of larger individuals), or if they leveled off. In a similar experiment, much larger (60–140 mm) *Pseudocaranx dentex* juveniles initially descended several meters before ascending to a much shallower "preferred depth," usually within 60 seconds (Kuwada et al., 2000). We did not observe such ascents following an initial descent, but we cannot rule out the possibility that they occur for individuals that swam below our safe diving depth (Fig. 5D).

Orientation in the pelagic environment is difficult for fish larvae because of the movement of the water column and the scarcity of reference points in a moving pelagic environment. Orientation is, however, necessary for the arrival of late-stage larvae at nursery habitat and can greatly influence dispersal trajectories (Shanks, 1995; Leis and Carson-Ewart, 2003). Two-thirds of the *C. ignobilis* larvae that we observed swam directionally, as opposed to swimming randomly. This is a somewhat smaller percentage than the 80–100% for directional individuals at the settlement stage for demersal coral reef fishes of similar size (Leis and Carson-Ewart, 2003). Neither the proportion of individual *C. ignobilis* that swam directionally, nor the precision of their directional swimming, increased with growth. The lack of ontogenetic change in individual orientation—in contrast to speed, endurance, and vertical distribution—indicates that orientation ability develops early (at less than 8 mm SL) in *C. ignobilis* larvae. Of course, orientation may improve in individuals larger than those we studied.

The offshore swimming direction of *C. ignobilis* larvae found off the west coast is similar to behavior reported for larvae of some other species at other locations (e.g., Leis et al., 1996; Leis and Carson-Ewart, 2003), but could, in fact, be orientation to the west, rather than offshore. Observations off the east coast would be required to separate the possibilities, and any such test would need to take into account the possibility of temporal factors. The lack of any directionality in Nan Wan Bay is possibly a result of the "U" shape of the bay. Such a bay, where "offshore" constitutes less than half of the possible swimming directions, and where west is onshore, may present challenges to orientation that are greater than those present off an open coast. Alternatively, a bay may offer characteristics that would induce larvae to remain, rather than swim away as they did off the more open coast. Or, older larvae may prefer inshore environments, whereas younger ones do not. The important points, however, are that larvae of 8–15 mm SL demonstrated orientated swimming in the field and that smaller larvae swam in the same direction as larger ones. We can offer only speculation as to the types of cues that *C. ignobilis* may use to orient their swimming, and refer the reader to other sources for this information (e.g., Kingsford et al., 2002; Leis and McCormick, 2002). Our observations on *C. ignobilis* support other research showing that orientation behavior in fish larvae can be location-dependent (Leis et al., 1996; Stobutzki and Bellwood, 1998; Leis and Carson-Ewart, 2003), and if so, this feature add a further complication for attempts to model dispersal.

Our unplanned *in situ* observations of behavior shed light on little-known aspects of the early life history of *C. ignobilis*, which are otherwise difficult to study. Feeding activity by 8–18 mm larvae of *C. ignobilis* was common while they were swimming, as has been found with other species (Leis and Carson-Ewart, 1998). The only larva to encounter a large pelagic fish reacted in the same way as that reported for other species, namely with the apparent goal of moving away from the potential large predator before the small fish could be readily detected (Leis and Carson-Ewart, 2001). Such behavior in a reared individual with no experience with piscivorous fishes indicates that the behavior is not learned. Many carangids associate with jellyfish medusae when small (Shojima, 1962); therefore the brief association we observed between a jellyfish and a 10-mm *C. ignobilis* was not unexpected. *Caranx ignobilis* is considered to be reef-associated during some periods of its life history, but individuals of 9–13 mm do not seem to be inclined to associate with coral reefs. Unlike the larvae of many demersal reef fishes (Leis and Carson-Ewart, 2002), the larval *C. ignobilis* that we observed made no attempt to settle and showed no interest in coral reefs. If anything, *C. ignobilis* moved away from the coral reefs they encountered, although this behavior is not uncom-

mon in larvae of other species (Leis and Carson-Ewart, 1999, 2002). We observed one individual penetrate a thermocline, indicating not only a tolerance for rapid temperature change, but also, that the thermocline is not a barrier to vertical movement for *C. ignobilis*, as has been proposed sometimes for larvae of other species (e.g., Gray and Kingsford, 2003).

We used reared larvae in our study and it is possible that the behavior we observed may have differed from that of wild individuals. Results of studies comparing wild and reared individuals have been inconsistent. Some studies have shown large differences in behavior of reared and wild fishes, the most marked of which involve learned interactions with predators (Brown and Laland, 2001). Differences in swimming performance (in both directions) have been documented in some studies, but not others, or have been present at some developmental stages but not others (e.g., Blaxter, 1975; Dunmall and Shreer, 2003; Smith and Fuiman, 2004). Even if differences in predator-related behavior exist, swimming and orientation are presumably less dependent on experience and learning, and there is less reason to expect them to differ as well. The possibility that reared larvae of *C. ignobilis* may behave differently from wild larvae cannot be entirely dismissed, but the fact that *C. ignobilis* larvae were reared in conditions approaching those found in the field (but with the absence of predators)—kept in large outside ponds at an aquaculture farm and fed a natural assemblage of zooplankton—would presumably make large differences in behavior with their wild counterparts less likely. Unfortunately, we did not have access to wild *C. ignobilis*, and therefore we could not make direct tests; moreover, little is known of behavior in other carangid larvae upon which we might base comparisons.

Caranx ignobilis apparently schools when young (Myers, 1999), and the size range of larvae we studied overlapped with that at which schooling begins in other carangid species (Masuda and Tsukamoto, 1998). We did not attempt to observe schooling in *C. ignobilis*, but it is conceivable that some of the aspects of behavior may differ between individuals that are schooling and those that are solitary.

We observed strong ontogenetic changes in behavior of *C. ignobilis* across a size range of 8 to 18 mm SL. At any size, there was usually a wide range of performances present, and the best performers were able to swim much better than average performers. Given the very high mortality rates experienced by marine fish larvae, the average larva at any given size is unlikely to survive (Cushing, 1990), and it may be only the exceptional performers that do survive. Therefore, it may be more appropriate to use values for the best performers than for average performers in models of dispersal or survival. Increases in swimming abilities with growth were most marked, and significant swimming abilities would probably be present, in larvae as small as 5 mm SL based on extrapolation of performance at size relationships. Ontogenetic changes in vertical distribution behavior were more complex and difficult to interpret, but depth selection seemed to be more variable (both within and among individuals) in larger larvae. We found that orientation behavior of small *C. ignobilis* was already developed and did not increase ontogenetically, although the direction they swam differed between locations. Behavior in small *C. ignobilis* was complex and swimming abilities were well developed. These behaviors are capable of strongly influencing survival and dispersal and show that the larvae of some pelagic fishes have behavioral capabilities similar to those recently documented for larvae of demersal reef fishes (Leis and McCormick, 2002).

Acknowledgments

We thank the Director of NMMBA, Lee-Shing Fang, for the opportunity to work at NMMBA and his staff for their excellent cooperation, particularly Chao-Yuan Chung for assistance in the wet laboratory. Our work could not have proceeded without the assistance of Colin Wen and Kun-Ping Kan in all phases of the work. Li-Hua Chao generously introduced us to many Taiwanese aquaculturists and spent many hours helping us obtain larvae. Mark Brown assisted ably, especially with laboratory work. Ray-Ming Chen, our dive boat skipper, made possible our field work, and Bill Watson helped with literature. This research was supported by an ARC Discovery Grant (DP0345876), and a DST International Science Linkages Grant (IAP-IST-CG03-0043) to JML, and by the Australian Museum. Reiji Masuda made constructive comments on the manuscript.

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Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life

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Abstract—Data storage tags (DSTs) were applied to Atlantic salmon (*Salmo salar* L.) smolts during their seaward migration in the spring of 2002 at a fish counting fence on Campbellton River, Newfoundland. Our objectives were to discover whether or not salmon smolts could carry DSTs and survive, whether or not useful data on thermal habitat could be obtained and interpreted, and whether or not salmon smolts moved vertically in the water column. Data were downloaded from 15 of the recovered tags and revealed the hourly water temperatures experienced by the fish for periods of 3 to 71 days. The data on the DSTs were analyzed for temperature patterns in relation to migration behavior and diurnal movement of the fish. While in the sea, the DSTs recorded night temperatures of 12.5°C, which were higher than day temperatures of 11.6°C; the record from moored recorders, however, indicated that sea temperatures actually declined at night. It is hypothesized that postsmolts avoid avian predators during daylight hours by positioning themselves deeper in the water column and that they were pursuing prey during the deeper vertical descents or ascents noted during the periods of more rapid changes in temperature.

Manuscript submitted 27 September 2004 to the Scientific Editor's Office.

Manuscript approved for publication 28 September 2005 by the Scientific Editor.

Fish. Bull. 104:415–428 (2006).

Our knowledge of the ecology of marine fish, and specifically salmon, at sea has recently been enhanced by information recovered from data storage tags (DSTs) and tracking tags (Sturlaugsson[1]; LaCroix and McCurdy, 1996; Wada and Ueno[2]; Godø and Michalsen, 2000; Reddin et al., 2004). Direct tracking, although valuable, has a number of shortcomings, including the usually short duration of tracking because of the requirement to follow the fish. This short-term tracking often results in interrupted data streams and the added concern that the actual tagging may affect, at least in the short term, the subsequent behavior of the fish (LaCroix and McCurdy, 1996; Walker et al., 2000). Studies of salmon at sea over long periods require new tools and several authors have noted that DSTs are among the least expensive methods of answering some of the questions posed regarding the sea life of salmon. Also, the near extirpation of some stocks, particularly in the Inner Bay of Fundy area of Canada and Maine, U.S.A, requires an explanation of the causative factors (Boehlert, 1997; Anon.[3]; Friedland et al., 2001; Reddin et al., 2004). DSTs should be able to provide better information on the natural behavior of individual fish, their specific habitats, and location over the period of their residence in the sea because of the longer period that information can be collected.

On both sides of the North Atlantic, attention has been recently focused on the downturn in Atlantic salmon stocks and the potential cause or causes (Nickson[4]; Mills[5]; DFO[6];

[1] Sturlaugsson, J. 1995. Migration study on homing of Atlantic salmon (*Salmo salar* L.) in coastal waters W-Iceland—depth movements and sea temperatures recorded at migration routes by data storage tags. ICES C.M. (council meeting) 1995/M: 17, 13 p.

[2] Wada, K. and Y. Ueno. 1999. Homing behavior of chum salmon determined by an archival tag. NPAFC (North Pacific Anadromous Fish Commission Doc. 425, 29 p.

[3] Anon. 1998. Report of the Study Group on ocean salmon tagging experiments with data logging tags. ICES C.M. (council meeting) 1998/G: 17, 34 p.

[4] Nickson, Sir D. 1991. Chairman's report, Atlantic Salmon Trust, progress report, December 1991, 1 p. Atlantic Salmon Trust, Moulin, Pitlochry, Perthshire, Scotland PH16 5JQ.

[5] Mills, D. (ed.). 1996. Enhancement of spring salmon. Proceedings of a one-day conference held in the rooms of the Linnean Society of London; 26 January 1996, 135 p. Atlantic Salmon Trust, Moulin, Pitlochry, Perthshire PH16 5JQ Scotland.

[6] DFO (Dept. of Fisheries and Oceans). 1998. Atlantic salmon abundance overview for 1997. DFO CSAS (Canadian Stock Assessment Secretariat), Stock Status Report D0-02(1998), 22 p.

O'Neil et al.[7]; Anon.[8]). Many authors have noted that information on the sea life of Atlantic salmon (*Salmo salar* L.) may aid in our understanding of the recent increased mortalities that occur at sea compared to those experienced in the 1970s (Mills, 1989; Reddin and Friedland, 1993; Dempson et al.[9]; Jacobsen, 2000; Reddin et al., 2000). In the southern end of the range of Atlantic salmon in North America, declines have been so severe that some stocks are now threatened with extinction and others are currently considered to be extirpated (Marshall et al.[10]). The recent listing of seven salmon stocks in the State of Maine under the U.S. Endangered Species Act and in rivers in the upper Bay of Fundy further underscores the urgency to understand more completely the entire salmon's life history, including the period spent in the ocean. Although the cause (or causes) is unknown, the continued declines in abundance appear directly related to increased mortality at sea, perhaps from predation (DFO, 1998; Cairns and Reddin[11]; O'Neil et al.[7]).

New techniques have recently been applied to the study of salmon in the sea on both sides of the North American continent for Pacific and Atlantic salmon, and recommendations have been made on their future use (Boehlert, 1997; Anon[3]). Although large scale experiments with complex tags are attractive, the high cost per tag and likelihood of low returns, in part due to reduced commercial fishing for Atlantic salmon, have indicated that a smaller scale experiment with inexpensive simple tags may be the best place to start (Anon.[3]). Reddin et al. (2004) demonstrated that these tags when applied to Atlantic salmon adults could provide insight into some aspects of salmon life history.

Overall, the objectives of the present study were 1) to determine if DSTs could be applied to Atlantic salmon smolts and if data could be successfully recovered, 2) to learn more about the thermal habitat of Atlantic salmon during its early marine life, and 3) to test the hypothesis of the commonly held assumption that salmon are mainly surface or near to surface dwellers. This article describes the results of the migration of Atlantic salmon smolts from Campbellton River, Newfoundland, in relation to sea water temperatures recorded by DSTs in 2002.

Materials and methods

Experimental site

Atlantic salmon smolts, defined by Allan and Ritter (1977) as juvenile salmon that are making the transition from freshwater to the marine environment, were obtained in 2002 for tagging from an enumeration fence on Campbellton River, Newfoundland (Fig. 1) where in past years, high numbers were available in early spring (Downton and Reddin[12]). Also, because Campbellton River has a counting fence that is suitable for obtaining counts of adult salmon as they re-enter freshwater, there was a strong possibility of recapturing a returning tagged salmon so that its tag could be recovered (Fig. 1). Smolt and adult salmon have been counted at Campbellton River annually over the last 11 years (O'Connell et al.[13]). In total, there were about 32,600 salmon smolts counted through the counting fence at Campbellton River in 2002, and of these, 311 (~1% of total smolts) were tagged and released with data storage tags (DSTs). Owing to the size and weight of the tags, only smolts over 20 cm fork length were selected for application of tags. Average length of tagged smolts was 25 cm compared to an average length **of** 18 cm for untagged smolts. Larger smolts were also purposely selected to increase probability of survival.

Tags

The data storage tags (DSTs), sometimes referred to as archival tags, used in this study were iB-4 tags (Maxim/Dallas Semiconductor Corporation, Sunnyvale, CA) and were repackaged for use on fish by Alpha Mach Devices Inc. (Mont St-Hilaire, Québec, Canada). The iB4 tags are small microprocessor-based data loggers embedded in green urethane on which is shown (at bottom right corner of tag) a return address, an identifying number, and the offer of a reward for return of the tag. The iB4 DST records temperature over a range of –5° to 26°C

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[12] Downton, P. R., and D. G. Reddin. 2004. Status of Atlantic salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2003. DFO, CSAS Res. Doc. 2004/043, 49 p.

[13] O'Connell, M. F., J. B. Dempson, C. C. Mullins, D. G. Reddin, C. E. Bourgeois, T. R. Porter, N. M. Cochrane, and D. Caines. 2003. Status of Atlantic salmon (*Salmo salar* L.) stocks of insular Newfoundland (SFAs 3-14A), 2002. CSAS Res. Doc. 2003/002, 63 p.

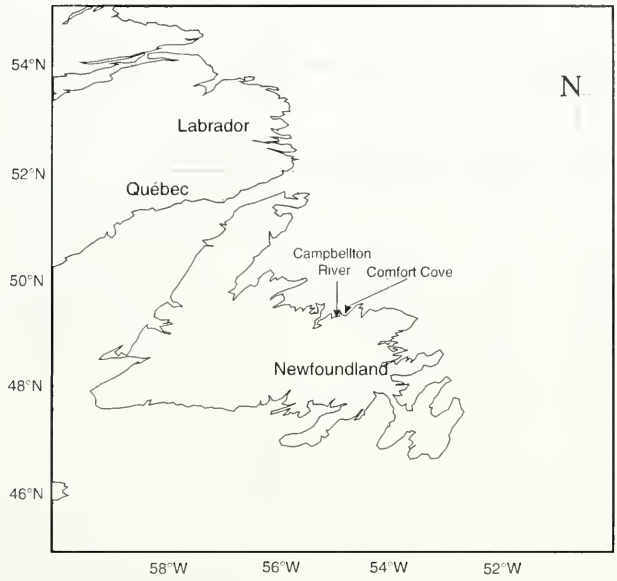

Figure 1

Map of Newfoundland, Labrador, and Québec showing the release location at Campbellton River for Atlantic salmon (*Salmo salar*) smolts with data storage tags attached.

with a precision of ±1°C and an accuracy of 0.15°C. The iB4 data storage tag will store up to 2048 readings but the number of data recorded by each tag depends on the length of time that the tag was at large and the sampling rate of the tag. Our iB4 tags were set to start on the day of tagging and record a temperature every hour—a sampling rate that would allow for 85 days of temperature recordings. Tags were calibrated by the manufacturer and checked for accuracy on return. A tag weighs 5.5 g in air and less than 2.6 g in water, is approximately 24 mm by 17 mm by 8 mm, and has a hole at either end for attachment to a fish. Tag programming, data acquisition, and data downloading were achieved by the user with a connecting clamp interfaced to the serial adapter on any standard IBM compatible computer. No correction for drift in the time function was made because of the short period over which the experiment took place (Walker et al., 2000; Reddin et al., 2004). Tags were attached to salmon smolts by using a double-wire (0.32 mm stainless steel) bridal that was passed through the dorsal musculature and that was anchored to the fish by means of a backing plate on the opposite side of the fish. A reward of $10 Canadian was offered for the return of the tag. The smolts were anaesthetized with clove oil, tagged, and placed in holding tanks in the river and given an approximate 10-hour recovery period before release in the evening on the downstream side of the counting fence. All smolts survived the tagging process. From 311 salmon tagged and released, 15 DSTs were recovered with data intact. All tagged fish were recovered during the year of tagging.

Data analysis

Temperature data recorded by the recovered DSTs were analyzed and compared to oceanographic and freshwater temperature data collected during the summer of 2002. The freshwater data was recorded by a Hugrun temperature recorder (Hugrun, Sidumuli 13, Reykjavik 108, Iceland) placed in the trap at the Campbellton River counting fence, and the sea temperatures came from Hugrun recorders placed just outside the estuary of Campbellton River at 8 m depth and from another at Comfort Cove at 10 m, both reported by Colbourne[14] (Fig. 1). Periods of daylight and darkness were estimated from the U.S. Navy Observatory[15] online photoperiod calculator. Latitudinal and longitudinal positions

[14] Colbourne, E. 2003. Physical oceanographic conditions on the Newfoundland and Labrador Shelves during 2002. DFO, CSAS Res. Doc. 2003/020, 57 p.

[15] U. S. Naval Observatory, Astronomical Observations Department. 2004. Website: http://aa.usno.navy.mil/data/docs/RS_OneDay.html [accessed on 7 March 2006.]

used to calculate sunrise and sunset for individual fish were based on the latitude and longitude at the mouth of Campbellton River. Although it varies by date, day at the latitude of Campbellton River during summer generally occurs from 0500 hours to 2300 hours and night occurs from 2300 to 0500 hours local time. Each individual temperature record from the tags in Greenwich Mean Time (GMT) was then coded to either day or night. Some salmon smolts in Newfoundland return to their home rivers within a couple of months of migrating to sea as precocious postsmolts and as postsmolts cannot travel extensively from the area of the river mouth, so that the river mouth provides a proxy position to determine day length (Downton and Reddin, 2004). Standard weeks were assigned with the Microsoft Excel function WEEKNUM. The analysis of variance technique used to test for temperature differences between fish was the PROC MIXED procedure in SAS (SAS Institute Inc., Cary, NC) The model treated tag as a random rather than a fixed variable. Day temperatures were compared to those at night and any diurnal vertical movements were considered to be reflected by sudden changes in temperatures. Newfoundland coastal waters always exhibit vertical stratification in late spring and early summer.

Results

Tag and data recovery

In total, temperature records were recovered from 15 of the 18 tagged Atlantic salmon smolts for an overall return rate of 5.8% (Table 1). Of the 18 recovered tags, 13 came from herring nets during the same summer that the fish were released. Average days free for those DSTs recovered in herring bait nets was 14 days and all were recovered within Indian Arm into which Campbellton River flows. In addition, two were recovered at the counting fence, one was recovered during a swimming survey of the lower portion of the river, one was angled, and another was found by a swimmer a full year after the fish was tagged and released. The great number of tags recovered in herring gear was due to tags becoming entangled in the nets. The longest period of recorded water temperatures while fish were free swimming was 71 days and the shortest was 3 days (Table 1). All tags were recovered during the first summer after their release, except the one found by the swimmer.

Water temperature profiles

Temperatures were recorded every 60 minutes for all recovered tags. The overall sampling frequency or the number of data points collected per tag ranged from a low of 32 for DST257 to a high of 1681 for DST45 and the second longest was for DST267 with 1373 (Table 1). The most complete records were recorded by DSTs 45 and 267 because the fish to which they were attached spent the least amount of time in freshwater and returned to freshwater after spending a minimum of eight weeks at sea. Both of these fish returned at 0+ sea age, a trait which is observed in about 15% of the salmon returning to Campbellton River in recent years (Downton et al., 2004). The water temperature profiles from the DSTs revealed a complex pattern of daily variations (Figs. 2–4). A number of points of interest can be made from the individual DST records. The temperature records from the DSTs when compared to local freshwater and marine temperatures allowed the time of day to be ascribed for most fish when the transition from the river to sea occurred (Fig. 3). The records indicated that 8 out of 13 fish made the transition from freshwater to the sea during daylight, whereas both fish recovered at the counting fence after spending time at sea re-entered freshwater during the night. Because they had the longest period of free swimming activity recorded on the DSTs, tags 45 and 267 were selected for further analysis including comparison for freshwater and sea temperatures (Fig. 3). Within the daily variations, temperature profiles from individual DSTs showed several prominent features:

1 a period of freshwater residence during which time the freshwater and DST temperatures corresponded closely, followed by entry into the sea at which time the temperatures recorded by the DSTs diverged from the recorded freshwater temperatures (Fig. 4, A and B);
2 a period of low variability in temperature fluctuations at the beginning of the marine record (with a coefficient of variation of less than or equal to 10%), continuing for at least a couple of weeks (Fig. 4C);
3 after the period of low variability, a series of rapid daily changes in temperature from either warm to cool or, for a few limited cases, from cool to warm (with coefficients of variation of greater than 30%) (Fig. 4, D and E) and during this period, DST temperatures sometimes varied by as much as 13°C over a couple of hours;
4 a distinct trend to increasing temperatures as the summer progressed which was due to gradual heating of the surface layer and deepening of the thermocline (Fig. 3); and
5 a series of steady temperatures near the end of the ocean period before entry into freshwater (with coefficients of variation of less then 12%) (Fig. 4F).

Between the periods of low temperature variability at the beginning and end of the various series, there was a period of rapid changes in temperature when the fish were assumed to have dived deeper in the water column, followed by ascents to near surface. The frequency of these rapid changes in temperature provides some information on the number of dives per day which numbered between 1 and 3 and may be a proxy for the length of time spent feeding and chasing after prey or fleeing from predators.

Table 1

Release and recovery details for eighteen iB-4 data storage tags (DSTs) applied to Atlantic salmon (Salmo salar) smolts at Campbellton River, Newfoundland, 2002. N/A= data were not available.

DST number	Number of records	Date and time tag was turned on	Date and time when tag was recovered	Fork length (cm)	Return date	Days free	Comments
22	327	5/17/02 8:20	5/17/02 8:20	22.0	spring, 2002	15	Caught in herring bait net in Indian Arm Tag found 25 m below counting fence site
43	N/A	5/19/02 7:59	5/19/02 9:28	24.0	24 May 2002	—	No fish was attached to tag
45	1681	5/19/02 8:06	5/19/02 9:36	28.0	28 Jul 2002	71	Caught at the upstream counting fence
55	N/A	5/19/02 8:30	5/19/02 10:19	27.0	03 Jul 2003	—	Found in estuary by swimmer
74	N/A	5/21/02 8:46	5/21/02 10:23	23.0	spring, 2002	—	Caught in herring bait net in Indian Arm
84	180	5/23/02 10:40	5/23/02 15:32	26.0	spring, 2002	8	Caught in herring bait net in Indian Arm
97	305	5/24/02 8:16	5/24/02 10:30	24.0	spring, 2002	14	Caught in herring bait net in Indian Arm
98	588	5/24/02 8:21	5/24/02 10:30	27.5	spring, 2002	26	Caught in herring bait net in Indian Arm
103	302	5/24/02 8:36	5/24/02 10:30	26.0	spring, 2002	14	Caught in herring bait net in Indian Arm
107	634	5/24/02 9:09	5/24/02 10:30	26.0	spring, 2002	28	Caught in herring bait net in Indian Arm
129	562	5/26/02 8:21	5/26/02 11:00	25.0	spring, 2002	25	Caught in herring bait net in Indian Arm
195	213	5/30/02 9:08	5/30/02 10:48	26.0	spring, 2002	10	Caught in herring bait net in Indian Arm
238	133	6/1/02 8:12	6/1/02 10:14	25.0	spring, 2002	7	Caught in herring bait net in Indian Arm
245	129	6/2/02 7:35	6/2/02 9:04	25.0	spring, 2002	6	Caught in herring bait net in Indian Arm
247	401	6/2/02 7:39	6/2/02 9:12	24.0	19 Jun 2002	17	Angled upstream
257	32	6/2/02 8:07	6/2/02 9:56	25.0	spring, 2002	3	Caught in herring bait net in Indian Arm
267	1373	6/2/02 8:29	6/2/02 10:49	34.0	30 Jul 2002	59	Recovered by upstream counting fence
293	240	6/4/02 6:59	6/4/02 9:50	26.0	spring, 2002	11	Caught in herring bait net in Indian Arm

Thermal ecology

A comparison of temperatures for night and day for the two tag recoveries with detailed data indicated differences between daily night and day temperatures for weeks 24 to 29 (11 June–22 July) (Fig. 5). The tagged salmon appeared to be at lower temperatures during the day than at night. Although there were only slight differences between day and night for the cumulative temperatures in some weeks (i.e., week 24 [11–17 June]), for others the differences were quite large (i.e., week 27). These differences were reflected in the overall mean of 12.5°C at night compared to the overall mean of 11.6°C during the day—values which are significantly different from each other ($t = -6.32$, $P<0.0001$) and which possibly reflect temperatures at different depths. Although there was some variation among fish, this pattern was gener-

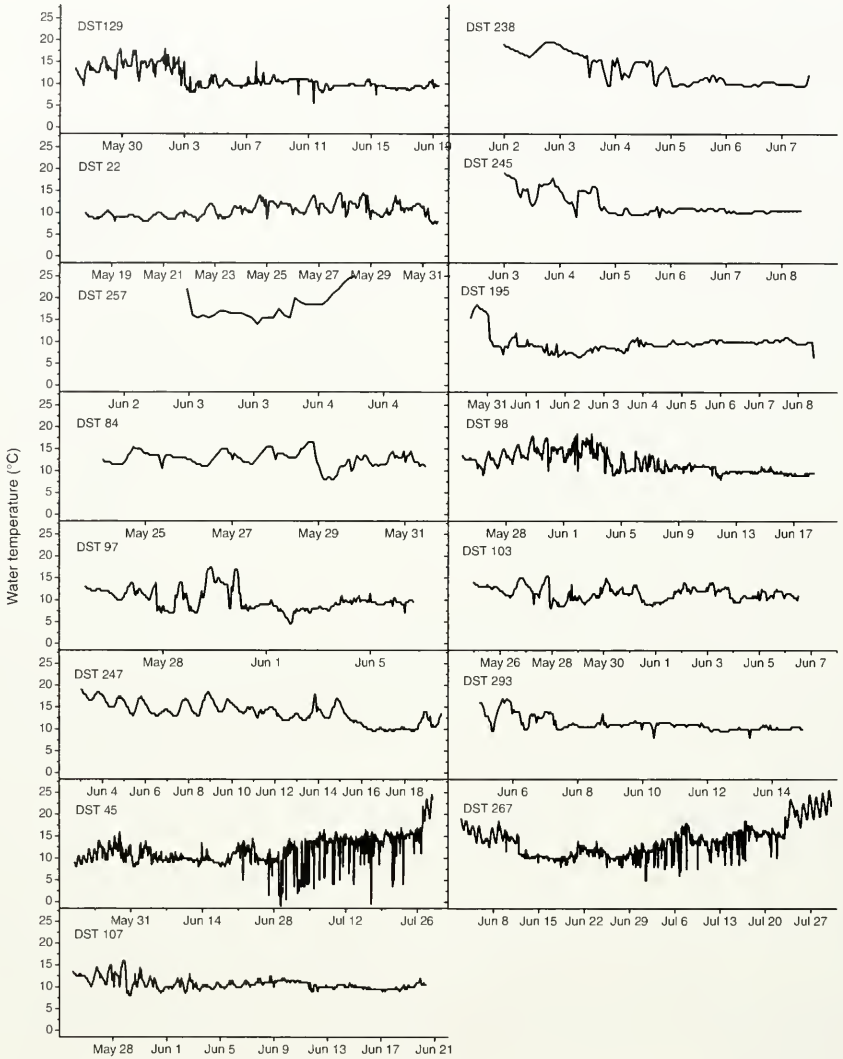

Figure 2

Hourly temperatures and dates recorded by 15 data storage tags attached to Atlantic salmon (*Salmo solar*) postsmolts at Campbellton River, 2002.

ally consistent. The cooler temperatures experienced by the fish during the day indicated that they were deeper in the water column during day than during the night. Diurnal trends in water temperatures also have to be considered because stream temperatures are generally warmer during the day than at night. Warmer temperatures during the day are generally the case for sea temperatures as well (t=5.00, P<0.0001) although less

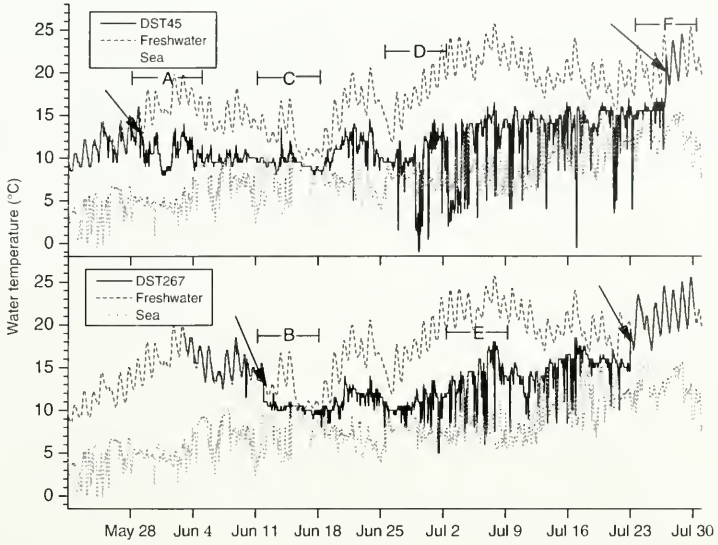

Figure 3

Hourly temperatures recorded by data storage tags on Atlantic salmon (*Salmo salar*) postsmolts versus date for tags 45 and 267 applied at Campbellton River, 2002. Also shown are water temperatures recorded at the trap in the Campbellton River counting fence and in the sea near the Campbellton River estuary, 2002. Arrows indicate time of departure from and entry to freshwater. Periods selected for further analysis are shown and labelled alphabetically from A to F and are shown in detail in Figure 4.

pronounced at greater depths. Because sea temperatures are lower at night than during the day and because the water temperatures experienced by the fish are warmer at night, it is likely that the fish are actively changing depths. Also, there were times when water temperatures declined or increased by 5°C but the temperature of the fish remained steady; this feature would indicate that the fish was actively seeking specific temperatures and changing position in the water column in order to find these temperatures.

The results of the mixed-effects ANOVA with data for weeks 24 to 29 from fish tags 45 and 267 indicated significant differences in temperature for week ($F_{5,1987}$=251.82, P<0.0001) and night-versus-day effects ($F_{1,2393}$=54.53, P<0.0001). Both smolts spent about 90% of the time in water temperatures ranging from 8° to about 15°C. Overall, mean temperature for day activities for both fish combined was 11.6°C and for night it was 12.5°C. Therefore, for all weeks for both fish, temperatures experienced during the day were generally lower than during the night. Whether these differences were due to choice or simply because the fish were in different locations and experiencing local water conditions is unknown.

The frequency distribution of water temperatures while the fish were in the sea showed a wide range, from below 0° to about 20°C (Fig. 6). This distribution was wider and included temperatures that were both colder and warmer than temperatures available in the estuary off Campbellton River at 8 m or at Comfort Cove at 10 m. The warmer temperatures in the estuary than those recorded by the sea recorders are possibly due to the fish being near the surface or shore (or to both factors). The DST temperatures were lower than freshwater temperatures, reflecting the sea temperatures rather than freshwater temperatures. The pattern for each fish presumably reflects a combination of individual preferences and the availability of specific water temperatures depending on the location of the fish at sea. The temperatures recorded by each tag reflect the time (season) of entry into the sea and the time of recapture, especially for those fish caught in fisheries while the fish were still at sea.

Discussion

The transition from freshwater to ocean life for Atlantic salmon (whether as smolts or kelts) can have a serious

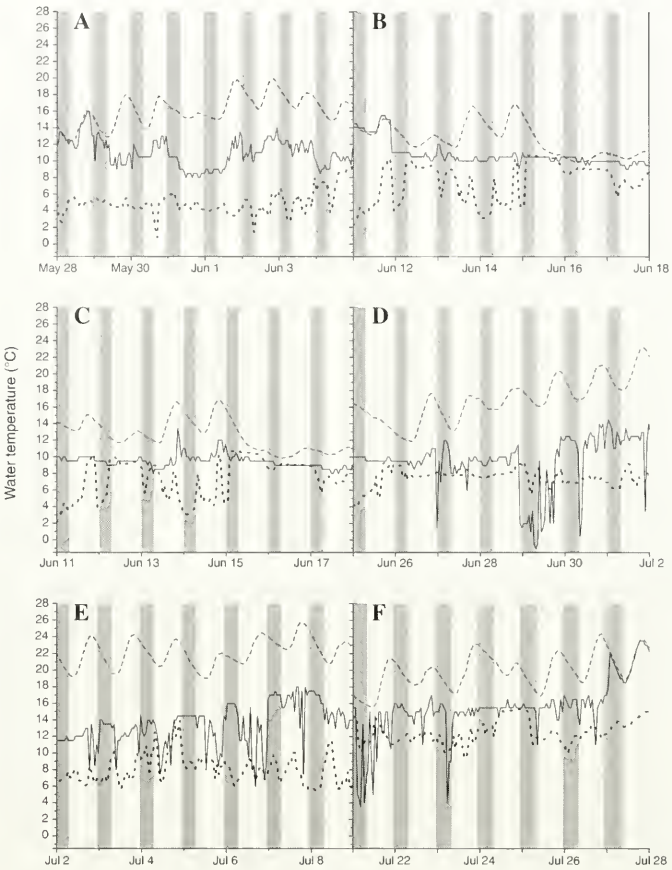

Figure 4

Comparison of day and night temperatures recorded hourly by data storage tags on Atlantic salmon (*Salmo salar*) postsmolts for selected periods of time. Night is shown in grey and day is shown in white. Solid lines are the DST temperatures; the dashed line represents freshwater temperature and dotted line represents sea temperature at 8 m. The periods A to F are shown on Figure 3 for each tag.

consequence for an individual fish, as well as be an important factor controlling year-class strength and abundance at the population level (McCormick and Saunders, 1987, McCormick et al., 1998). The transformation process from freshwater to salt water made by smolts is accompanied by changes in metabolic rate (Hoar, 1988) and increases in energy demands, which explain the need for the fish to immediately begin feeding. Levings (1994) concluded that of all the variables influencing survival of postsmolt salmon, temperature is particularly important. If they are to survive, individuals must quickly adapt to their new physical environment and be able to flee predators and seek prey. In spite of its presumed importance, the ecology of salmon smolts as they enter the marine environment is largely unknown. This article provides the first recorded results of temperatures experienced by salmon smolts as they enter the sea and provides insight into how postsmolts adapt to life at sea based on ambient temperature ranges and temperature choices made by the postsmolts. The

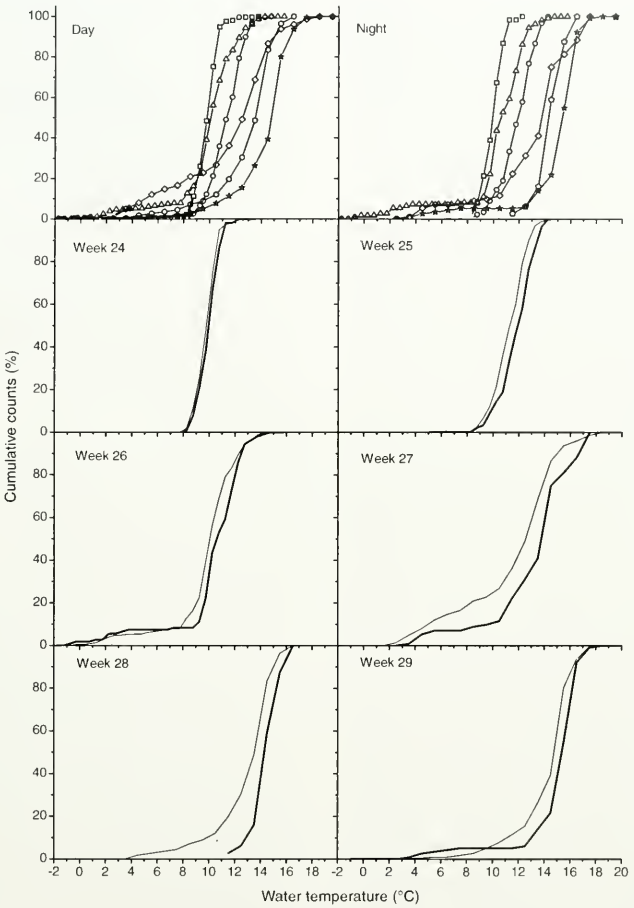

Figure 5

Difference between night and day temperatures recorded hourly by data storage tags and expressed as cumulative counts for weeks 24 to 29 from Campbellton River, 2002. Water temperatures are shown for six periods and for all day and night temperatures. Thin solid line is for daytime temperatures and thick line is for night time temperatures. In the multi-line graphs labelled "day" and "night," the square=week 24, the circle=week 25, triangle=week 26, polygon=week 27, dark pentagon=week 28 and the star=week 29.

temperature profiles collected by these data storage tags provide detailed information on the thermal habitat experienced by 15 Atlantic salmon postsmolts for periods ranging from a few days to about two months at sea. Temperatures recorded ranged from below 0° to nearly 20°C, although most of the time was spent in water from 8° to 15°C, probably near the surface.

Sigholt and Finstad (1990) and Handeland et al. (2003) reported that lethal sea water temperatures for both wild and farmed salmon smolts adapting to seawater occurred at very low and very high temperatures. At the lower end of the range in temperatures, some mortalities occurred at sea temperatures of 6–7°C, whereas at the higher end, mortalities occurred at temperatures

over 14°C, indicating that there may be environmental windows for successful transition of smolts into the sea at locations other than at the extreme edges of the temperature ranges documented by Power et al. (1987). Reddin and Friedland (1993) noted that during colder years with heavy ice flows along the northeast coast of Newfoundland, commercial catches and returns of salmon to rivers were lower, even though freshwater warming was occurring normally and they also noted that these low catch rates and returns may have been due to the mortality of postsmolts early in the marine phase. Our results from DSTs applied to Campbellton River smolts indicated that temperature-related mortalities, at least in 2002, were unlikely because the smolts spent little time in water colder than 7°C. Furthermore, because the only colder water present was deeper in the water column, salmon postsmolts were able to avoid it by remaining in the warmer surface waters. In 2002, there was little or no inshore ice at the time of the Campbellton River smolt migration as is sometimes present in other years when mortalities from cold water temperatures could occur.

It is interesting to note that temperatures recorded by the DSTs for the first few weeks after the smolts entered the sea were very similar to that experienced by salmon kelts tagged with DSTs also from Campbellton River (Reddin et al., 2004). In addition, the temperatures from tagged kelts when compared to temperatures from tagged smolts showed similar periods of stability just after entry of the salmon into the sea, as well as abrupt changes in temperatures consistent with deep diving activities. Although we did not know the precise geographic location of either group of fish, it appears that kelts and postsmolts are found initially in water of similar temperatures and behave in similar ways with respect to temperature. Because neither the postsmolts nor kelts started their deep diving activities for four weeks after sea entry, it may be that they were recovering from the transition process or that they may have been near shore where deeper depths are not available (or both these reasons may apply). Resolution of these questions will have to await the results from application of geolocation and depth-sensing tags.

Colbourne et al.[16], Friedland et al. (2003), Beamish and Bouillon (1993), and Downton and Miller (1998) and many others have examined relationships between environmental variables and the abundance of Pacific and Atlantic salmon and other fish species with a view of providing forecasts of future abundance but without any knowledge of what thermal regimes the fish actually use. Colbourne et al.[14] indicated that the goal of searching for relationships is important in order that

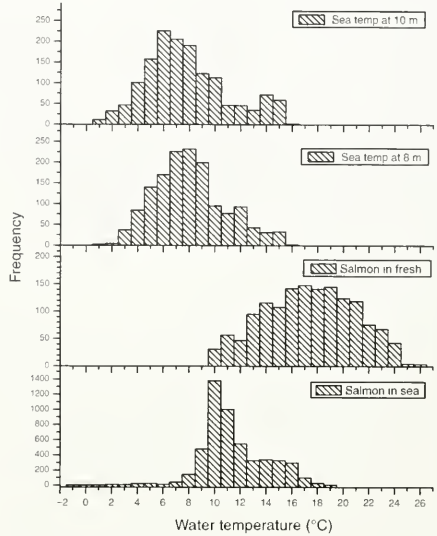

Figure 6

Frequency distributions for all temperatures recorded hourly at sea at 10 m depth (Sea temp at 10 m) and at 8 m depth (Sea temp at 8 m), and for salmon in freshwater from the DSTs (Salmon in fresh), and for salmon from DSTs while in the sea (Salmon in sea). All sea temperatures from the DSTs were used and the freshwater and marine temperatures are for the same time periods that the DST-tagged fish were in the sea.

influences of the physical ocean environment can be used to provide more accurate forecasts of stock abundance and ultimately so that they can be used to create management plans for various fisheries (Bisbal and McConnaha, 1998; Friedland, 1998). These predictions are currently used for both North American and European Atlantic salmon, for which abundance has been forecasted partly on the basis of environmental information (Anon.[8]). Physical conditions in the ocean have been shown to be related to mortality and growth of some other species (Brander, 1995; Dutil et al., 1999; Watanabe and Yatsu, 2004). Blackbourn (1993) and Downton and Miller (1998) have suggested that freshwater survival rates for some species of Pacific salmon are even related to SSTs experienced by potential spawners while still at sea, shortly before their return to freshwater. These studies and their importance clearly show the need for studies on the physical oceanography and ecology of fish at sea. For Atlantic salmon, Reddin and Friedland (1993) created a profile of sea temperatures, based on research vessel catch rates, that indicated that Atlantic salmon were commonly found in water at temperatures from 4° to 10°C. Reddin et al. (2004)

[16] Colbourne, E. B., E. G. Dawe, D. G. Parsons, E. F. Murphy, W. R. Bowering, E. L. Dalley, J. T. Anderson, J. B. Dempson, D. Orr, D. E. Stansbury, and G. P. Ennis. 2002. A preliminary review of environmental-stock relationships for some species of marine organisms in NAFO waters of the Northwest Atlantic. NAFO SCR Doc. 02/34, 21 p. Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

indicated that Atlantic salmon kelts tagged with DSTs were found where temperatures ranged from a low near 0° to over 25°C, although most of their time was spent in water of 5° to 15°C. This finding was similar to that for adults by Sturlaugsson[1] and Karlsson et al.[17] The present study indicates that salmon postsmolts are located mostly near the surface in water temperatures ranging from 8° to about 15°C. Because the temperatures experienced by kelt are somewhat warmer then those used in correlation studies of salmon growth and survival, it may be that our results will encourage other researchers to review the temperatures they use in such studies.

Prey items in the diet of adult Atlantic salmon are fairly well known revealing that Atlantic salmon are opportunistic feeders, feeding on whatever is abundant in the area (Reddin, 1988; Hislop and Shelton, 1993). Although food resources are still unknown for some regions, the prey species of smolts and postsmolts at sea has recently become an important area for research in the northeast Atlantic (Andreassen et al., 2001; Salminen et al., 2001; Rikardsen et al., 2004). Rikardsen et al.'s (2004) extensive analysis of postsmolt diet in eight fjords in Norway revealed extensive feeding on pelagic larval fish species and crustaceans, as well as substantial geographic and annual variation in prey diversity and feeding intensity. Furthermore, Levings (1994) summarized the diet of smolts and postsmolts in the estuarine and near-shore environments from publications by Power and Shooner (1966), Dutil and Coutu (1988), and Hvidsten et al.[18] which shows postsmolts feeding on gammarid amphipods and intertidal and land-based insects. Although diet information exists for postsmolts, the feeding mechanisms of postsmolts are unknown because there are few, if any, tracking studies in estuaries and the coastal areas. However, the new data on postsmolts early in their marine life that we have collected using DSTs can help us infer this information and the diet studies, although not specific to Newfoundland waters, indicate that salmon prey on pelagic fish larvae and crustacean species, some of which inhabit the deeper waters of the water column. Thus, it would appear that postsmolts in the present study and the kelts in a previous study (Reddin et al., 2004) were diving from surface waters to greater depths to obtain prey. The temperature profiles from the DSTs, compared to oceanographic data available from other studies (Colbourne[14]; Colbourne and Fitzpatrick[19]), indicate that these dives may be anywhere from 25 to 50 m in depth.

There is a tendency for postsmolts to be caught in the upper part of the water column, as evidenced by trawling for postsmolts at sea (Shelton et al., 1997; Holm et al., 2000; Rikardsen et al., 2004), by acoustic tracking of postmolts in fjords (Holm et al., 2000; Moore et al.[20]), and by net catches in surface waters (Dutil and Coutu, 1988; Reddin and Short, 1991; Thorisson and Sturlaugsson[21]). The temperature profiles from our DST-tagged postsmolts indicate that although most of their time is spent near the surface (and nearer the surface at night), salmon postsmolts undergo deeper dives, probably in search of prey. Deeper diving activities have been reported previously for salmon kelts also from Campbellton River by Reddin et al. (2004). The present study demonstrates that postsmolts also show the same type of behavior although the frequency of dives varies somewhat from fish to fish. Holm[22] et al. (2000) noted that salmon postsmolts caught in pelagic trawls in the Norwegian Sea were all caught during surface trawls; none were caught at deeper depths. Westerberg (1982) during coastal tracking studies noted that salmon made dives of short duration to greater depths; his results are similar to the results shown in our study.

Wada and Ueno (1999) listed three hypotheses to explain diving behaviour in Pacific salmon, viz. the salmon are making orientation for homing migration, for feeding, and for controlling body temperature. Reddin et al. (2004) suggested a fourth hypothesis: that the salmon are diving to avoid predators. Our conclusion is that the deep diving activities of salmon postsmolts (to as deep as 50 m) recorded by the DSTs, because of their frequent nature, are probably related to prey seeking and feeding. Reddin et al. (2004) further pointed out that there may be an energetic advantage for salmon to seek prey in cooler, deeper waters where prey are more abundant and then to return to warmer surface waters where their food can be digested more rapidly.

Ecological information can also be discerned from the temperature patterns provided by the DSTs. Ogura and Ishida (1995), Wada and Ueno (1999), Walker et al. (2000) and Reddin et al. (2004) all noted a period of more stable temperatures experienced at both the beginning and at the end of the temperature time series from the DSTs and concluded that the fish remained at the same

[17] Karlsson, L., E. Ikonen, H. Westerberg, and J. Sturlaugsson. 1996. Use of data storage tags to study the spawning migration of Baltic salmon (*Salmo salar* L.) in the Gulf of Bothnia. ICES C.M. (council meeting) 1996/M: 9, 15 p.

[18] Hvidsten, N. A., B. O. Johnsen, and C. D. Levings. 1993. Behaviour and feeding of emigrating salmon smolts in Trondheimfjord. Res. Rep. no. 164, 17 p. [In Norwegian.] Norwegian Institute for Nature Research, Trondheim, Norway, Tungasletta 2, 7485 Trondheim, Norway.

[19] Colbourne, E. B., and C. Fitzpatrick. 2003. Physical oceanographic conditions in NAFO subareas 2 and 3 on the Newfoundland and Labrador Shelf during 2002. NAFO (North Atlantic Fisheries Organization) SCR Doc. 03/14, 57 p. Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

[20] Moore, A., I. C. Russell, M. Ives, E. C. E. Potter, and C. P. Waring. 1998. The riverine, estuarine and coastal migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts. ICES CM 1998/N: 16, 11 p.

[21] Thorisson, K. and J. Sturlaugsson. 1995. Postsmolt of ranched Atlantic salmon (*Salmo salar* L.) in Iceland: IV. Competitors and predators. ICES C.M. 1995/M: 12, 9 p.

[22] Holm, M., I. Huse, E. Waatevik, K. B. Døving, J. Aure. 1982. Behaviour of Atlantic salmon smolts during the seaward migration. I. Preliminary report on ultrasonic tracking in a Norwegian fjord system. ICES CM 1982/M:7, 10 p.

location in the water column for some period of time, perhaps adjusting to the presence of the tag or to life in the sea (or to both). Furthermore, Reddin et al. (2004) noted that this period of temperature stability could be also due in some instances to the fish being near shore in shallow water where large scale vertical movements and their concomitant changes in temperature were not possible. This period of restricted vertical activity seemed to cease as the fish made its return migration towards freshwater. Our study indicates that in freshwater the water temperature recorded at the trap corresponds closely to the temperature recorded by the DST on the fish on its departure from the river and at its return. DST temperatures in freshwater follow the diurnal rhythm of warming and cooling of the river. In the sea, there is a period of stable temperatures with a diurnal rhythm that follows the daily warming and cooling. Next, the smolts began a period of fairly rapid descents and ascents in the water column during which temperatures rose and fell much more quickly then during the natural daily cycle. Also, night temperatures were warmer than day temperatures, in contrast to the daily warming and cooling cycle of the sea, indicating that smolts were higher in the water column at night then during daylight hours. The differences in temperatures between day and night may reflect avoidance of avian predators as suggested by Reddin et al. (2004) and Montevecchi et al. (2002). This finding is similar to that shown for adult chum salmon by Friedland et al. (2001) but contrasts with that reported by Shelton et al. (1997) who reported that no catches of postsmolts occurred at night during surface trawling in the northeast Atlantic. Because the records of trawling at night are sparse, we recommend that more effort should be put into night trawling in light of the information from our DST-tagged postsmolts.

In terms of our objectives, we have shown that Atlantic salmon smolts can carry DSTs, and that a sufficient number of tags with useful data on thermal ecology can be successfully recovered. The return rates were low and validated the preliminary use of the less expensive DSTs but were high enough that these experiments could be repeated elsewhere. The use of more expensive DSTs with geoposition and more environmental sensors will require methods to recover them at sea if sufficient tags are to be available to provide meaningful results. The thermal habitat used by Atlantic salmon is shown; postsmolts are found in water with temperatures ranging from 8° to about 15°C in the spring. Lastly, although we show from the water temperature records that salmon postsmolts are frequently found near the surface, it is also evident that they make frequent deep dives of short duration. We hypothesize that these deep dives may be directly related to feeding or to evasion from predators (or to both), as has been observed for kelts by Reddin et al. (2004).

Acknowledgments

We acknowledge the staff at the counting fence on Campbellton River, who assisted with tag application and data recording. The enthusiasm of Garnet Clarke and Roger Johnson who provided several helpful ideas on tag application is greatly appreciated. The comments provided by R. Poole and two anonymous reviewers are gratefully acknowledged.

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A prior for steepness in stock-recruitment relationships, based on an evolutionary persistence principle

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Abstract—Priors are existing information or beliefs that are needed in Bayesian analysis. Informative priors are important in obtaining the Bayesian posterior distributions for estimated parameters in stock assessment. In the case of the steepness parameter (h), the need for an informative prior is particularly important because it determines the stock-recruitment relationships in the model. However, specifications of the priors for the h parameter are often subjective. We used a simple population model to derive h priors based on life history considerations. The model was based on the evolutionary principle that persistence of any species, given its life history (i.e., natural mortality rate) and its exposure to recruitment variability, requires a minimum recruitment compensation that enables the species to rebound consistently from low critical abundances (N_c). Using the model, we derived the prior probability distributions of the h parameter for fish species that have a range of natural mortality, recruitment variabilities, and N_c values.

Manuscript submitted 20 July 2004 to the Scientific Editor's Office.
Manuscript approved for publication 30 September 2005 by the Scientific Editor.
Fish. Bull. 104:428–433 (2006).

Success in parameter estimation for stock assessment models often requires sufficient data and correct specification of prior distributions for the estimated parameters (Punt and Hilborn, 1997; Needle, 2002). This is especially true for successfully estimating stock-recruitment relationships with stock assessment models because there often are not sufficient data and there is considerable variability in stock-recruitment relationships. Even in the cases where there are sufficient data, these data can be very noisy and may not show a clear pattern for fitting stock-recruitment relationships (Hilborn and Walters, 1992; Williams and Shertzer, 2003; Munch et al., 2005). Yet, stock-recruitment relationships are important in making fisheries management decisions, especially for over-fished stocks such as widow rockfish (*Sebastes entomelas*), bocaccio (*Sebastes paucispinis*), and darkblotched rockfish (*Sebastes crameri*) along the west coast of the United States (He et al.[1]; MacCall[2]; Punt, 2003; Rogers[3]). Stocks with low values of steepness have low recruitment compensation; therefore stocks will take a long time to rebuild from over-fished status to desired management levels even though total allowable catches for these stocks are kept small (Mace and Doonan[4]).

In this study, we used a simple population model to derive prior distributions (referred to hereafter as "priors") for the steepness parameter (hereafter denoted h) (Mace and Doonan[4]). Prior distributions are probability distributions that represent existing information about parameters. The model was based on the principle that persistence of any fish species, given its life history and its exposure to recruitment variability,

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[2] MacCall, A. D. 2003. Status of bocaccio off California in 2003. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[3] Rogers, J. B. 2003. Darkblotched rockfish (*Sebastes crameri*) 2003 stock status and rebuilding analysis. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

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would require a minimum recruitment compensation to allow the species to rebound from low abundances. We argue that distribution of the h parameter for any species could be determined from its life history and recruitment variability. Using the model, we derived the prior distributions of h for fish species that have a range of natural mortality, recruitment variabilities, and low critical abundance (N_c) values.

Methods

In calculating steepness priors, we used a simple population model with a Beverton-Holt stock recruitment relationship:

$$N_{(t)} = N_{(t-1)}e^{-M} + \frac{N_{(t-1)}}{\alpha + \beta N_{(t-1)}} e^{\left(R_{(t)} - \frac{\sigma^2}{2}\right)}, \quad (1)$$

where $N_{(t)}$ = population size at year t;
M = natural mortality;
α and β = recruitment parameters; and
$R_{(t)}$ = the logarithm recruitment residual at year t that follows a normal distribution of $N(0, \sigma^2)$, where σ is recruitment variability (Hilborn and Walters, 1992).

This model produces recruitments that are log-normally distributed, and a correction factor of $\frac{\sigma^2}{2}$ is applied to $R_{(t)}$. The correction factor is included because it is commonly used in stock assessments. The Beverton-Holt stock recruitment relationship can be reparametrized as (Mace and Doonan[4])

$$\alpha = \frac{N_0}{R_0}\frac{1-h}{4h} \quad (2)$$

and

$$\beta = \frac{5h-1}{4hR_0}, \quad (3)$$

where N_0 = virgin abundance at equilibrium;
R_0 = virgin recruitment; and
h = recruitment steepness.

At equilibrium,

$$N_0 = N_0 e^{-M} + R_0 \quad (4)$$

and

$$R_0 = DN_0, \quad (5)$$

where D = death rate and is equal to $1 - e^{-M}$.

We now introduce the persistence criterion. For a given h, the persistence criterion is defined as

$$p(n,t \mid h,T) = \Pr\left\{N_{(s)} > N_c \text{ for all } t \le s \le T \mid N_{(t)} = n\right\}, \quad (6)$$

where T = a time far into the future;
n = a specific value of population size; and
N_c = a critically low level of abundance, below which the population would have very high probability of extinction.

At $t = T$, $p(n,T|h,T) = 1$ if $n > N_c$ and $p(n,T|h,T) = 0$ otherwise. In addition, $p(n,t|h,T)$ satisfies the boundary condition that $p(N_c,t|h,T) = 0$ for all t.

For times previous to T, $p(n,t|h,T)$ satisfies the stochastic iteration equation (Mangel and Clark, 1988; Clark and Mangel, 2000)

$$p(n,t \mid h,T) = E_{R_t}\left\{p\left(ne^{-M} + \frac{n}{\alpha(h) + \beta(h)n} e^{R_t}, t+1 \mid h,T\right)\right\}, \quad (7)$$

where E_{R_t} denotes the expectation over the stochastic processes associated with recruitment. We have indicated that the Beverton-Holt parameters depend upon steepness (as Eqs. 2–5 show, they also depend upon mortality M, which we hold to be a fixed value).

Because the recruitment uncertainty is normally distributed and Equation 7 cannot be evaluated analytically, we used a discrete distribution for R_t ($=R_{(t)} - \frac{\sigma^2}{2}$) into K (=61) uniformly spaced values (r_k) between -3σ and 3σ, so that

$$\Pr\{R_t = r_k\} = \frac{\exp\left(-\frac{r_k^2}{2\sigma^2}\right)}{\sum_{j=1}^{K} \exp\left(-\frac{r_j^2}{2\sigma^2}\right)}. \quad (8)$$

The iteration equation then becomes

$$p(n,t \mid h,T) = \sum_{k=-3\sigma}^{k=3\sigma} \Pr\{R_t = r_k\} \left\{p\left(ne^{-M} + \frac{n}{\alpha(h) + \beta(h)n} e^{r_k}, t+1 \mid h,T\right)\right\}. \quad (9)$$

We solve Equation 9 backwards in time, starting at $t = T-1$ (Mangel and Clark, 1988; Clark and Mangel, 2000) until reaching $t = 1$. Assuming that the population starts at the deterministic steady state ($n = N_0$), we can then calculate the prior probability for each h value using Equation 9. Because h is bounded between 0.2 and 1, we used an interval of 0.005 so that a total of 161 solutions of Equation 9 are needed to produce the prior probability for h. We then used a logistic equation to fit 161 prior probability values to produce a derived h prior curve $\{\phi(h)\}$:

$$\phi(h) = \frac{\theta_1}{1 + \frac{(\theta_1 - \theta_2)}{\theta_2} e^{-\theta_3 h_1}}, \quad (10)$$

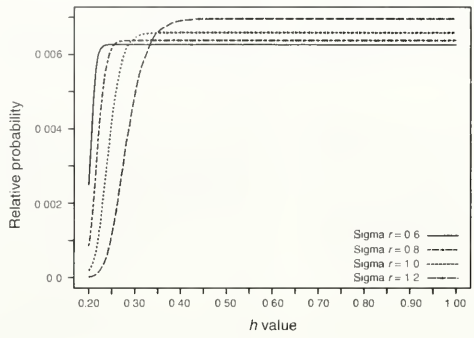

Figure 1

Relative probability distributions of the steepness (h) prior for four different σ values with the parameter setting M = 0.15, $N_c = 0.1N_0$, and T = 500 years.

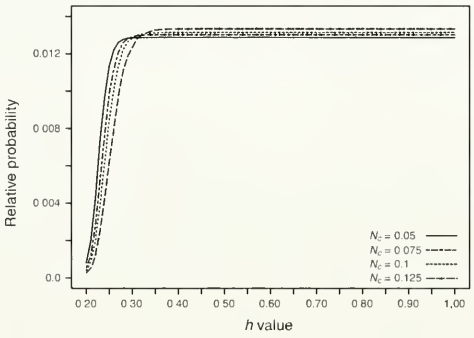

Figure 2

Relative probability distributions of the steepness (h) prior for four different N_c values with the parameter setting M = 0.15, σ = 1.0, and T = 500 years.

where $$h_1 = \frac{h-0.2}{0.8} \quad (11)$$

and θ_1, θ_2, and θ_3 are parameters for a logistic equation.

Note that the derived h priors produced above are relative probabilities, but that is what is needed for the assessment models and Bayesian priors.

Results

Derived h prior curves for M = 0.15, $N_c = 0.1N_0$, and T = 500 years at four different values of recruitment variability (σ) are shown in Figure 1. In general, the prior probability of h increased rapidly at low h values, and then remained at constant values at high h values. As expected, when recruitment variability (σ) increased, h values were higher to compensate for higher recruitment variability (Fig. 1). Table 1 shows parameter values of logistic curves fitted to derived h prior distributions as natural mortality (M) ranged from 0.05 to 0.7 and recruitment variability (σ) ranged from 0.2 to 1.6. These fitted curves would be convenient to use in stock assessment models for given natural mortality and recruitment variability, and values can be interpolated for intermediate cases. Derived h prior curves for four N_c values were plotted (Fig. 2). The figure shows patterns similar to those for recruitment variability, namely that as N_c values increase, h values are higher to increase recruitment potential for the population. Derived h prior curves for four natural mortality (M) values (M=0.1, 0.15, 0.3, and 0.5, respectively) are shown in Figure 3. As M values increase, h values also increase.

Discussion

This article presents a simple modeling approach that allows one to use life history criteria to derive steepness priors for a fish stock where no sufficient historical data could be used to establish reasonable stock recruitment relationships. The model used in this article requires a few assumptions, most of which could be inferred from the life history of the species. However, there is a shortcoming in our approach: a simple population model is used to derive h priors and then applied to the stock assessment model that is an age-structured population model. To derive h priors by using age-structured models would require some age-specific parameters, such as fecundity, growth, and possibly age-specific natural mortality rates. That is, "prior" information on these parameters for age-structured models is needed but in many cases they are not readily available (if they were, the entire stock assessment would be much easier). The parameters for age-structured models could be borrowed from stock assessment models, but applying priors back to stock assessment models could be deemed to be "double" uses of data (Minte-Vera et al., 2005). Our simple population model approach has been widely used in many other applications, such as in computing extinction risk in conservation biology (Hakoyama et al., 2000) and in simple production models in fisheries assessments (MacCall, 2002). In these applications, simple (non–age-structured) models were used for populations that are known to have age- or size-structures.

Although there are only a few parameters needed for the model, there are uncertainties in choosing ranges of values for each parameter. One of the important parameters in determining the priors is N_c, the parameter

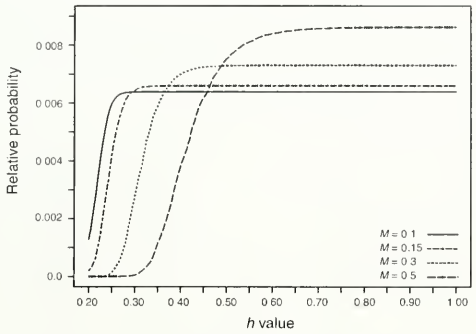

Figure 3

Relative probability distributions of the steepness (h) prior for four different natural mortality (M) values with parameter setting σ = 1.0, N_c = 0.1N_0, and T = 500 years.

characterizing critical abundance. This parameter is more or less a theoretical concept that defines the lowest population abundance deemed to be viable, and its value interacts with the time horizon, T. Although we used a relatively large value of N_c, the associated time horizon was short (T=500 yr) in the evolutionary time scale. Because the stock-recruitment dynamics near the origin are nearly linear, a relatively large value of N_c is approximately equivalent to using a lower value of N_c over a longer time horizon. Also, Mangel and Clark (1988) showed that once the time horizon is sufficiently large, the distributions have the same shape and become stationary. Test runs on our models with large values of T (T=3000 yr) showed almost the same results. In a complex marine environment like that of the U.S. west coast, it would be very difficult to determine "true" values of N_c and T, which could be, for example, at a level where the Allee effect is likely to take place and over a time scale of major environmental change, respectively. However, the results indicated that the model is not very sensitive to the N_c values (Fig. 2). For a range of N_c/N_0 values from 0.05 to 0.125, the prior probability curves were very similar. In contrast, recruitment variability (σ) had much greater effects on the distributions of the prior probability (Fig. 1). As recruitment variability increases, minimum h values need to be significantly higher in order to ensure population viability. Stock assessment reports on other west coast groundfish species have indicated a very high recruitment variability in the past few decades, such as for bocaccio, (σ=1.0, MacCall[2]), and darkblotched rockfish, (σ=0.85, Rogers[3]). However, some recent stock assessment models for the west coast groundfish species have used a lower value of σ, such as 0.6 (Punt, 2003). In our example, if lower values of σ are used, the derived h prior curves will be very flat for h>0.23 (Fig. 2), indicating that the population would be sustainable with very low h values.

Other methods for deriving h priors include using expert opinion, borrowing values from other taxonomically or ecologically related species, and using regional meta-analysis (Myers, 1998, 2001; Chen and Holtby, 2002; Dorn, 2002; Millar, 2002; Myers et al., 2002). For example, Myers et al. (2002) used an empirical Bayesian approach to derive prior distributions for steepness for nine species. As compared to our method, their method, based on a combined method of taxonomic and ecological criteria, still requires the collection of biological data from related species, as well as expert opinions on the life history of each species, which are somewhat "subjective" values. Dorn (2002) used Bayesian meta-analysis to derive stock-recruitment relationships for a group of west coast groundfish species. He used the results from the previous stock assessments for widow rockfish and other west-coast groundfish species and indicated that the prior distribution for steepness for widow rockfish could have a median value around 0.72 and a probability of 0.0033 for $h \leq 0.225$. This result could indicate that our method is more conservative because our method indicates much lower median value for widow rockfish-like species. Minte-Vera et al. (2005) also suggested that the priors derived by Dorn (2002) might not be appropriate for stock assessments that include the same data that were used in the meta-analysis to derive priors.

We believe that the method used in our study provides a scientific way of estimating the prior for steepness and avoids the pitfall of imposing a preconception of what the true distribution is thought to be. For example, it seems reasonable that very high values of h will not be likely because of tradeoffs between individual survival

Table 1

Parameter values of logistic curves fitted to derived h prior distributions for different natural mortality (M) and recruitment variability (σ). Parameters are listed in the order of θ_1, θ_2, and θ_3 (see Eq. 10). For some combinations of natural mortality and recruitment variability, distributions were uniform or could not be fitted.

Recruitment variability	Natural mortality 0.05	0.1	0.15	0.2	0.25	0.3	0.4	0.5	0.6	0.7
0.2	Uniform distribution	Uniform distribution	Uniform distribution	Uniform distribution	Uniform distribution	1.0000 669.60 0.9289	1.0000 443.00 0.8046	1.0000 306.13 0.6662	1.0000 282.66 0.5015	1.0000 278.16 0.3724
0.4		Uniform distribution	0.9994 139.90 0.9800	1.0000 248.40 0.7973	1.0000 223.60 0.5585	1.0000 196.43 0.3739	0.9999 199.3 0.2146	0.9999 182.22 0.08619	0.9999 157.82 0.04454	0.9997 148.63 0.02264	0.01154
0.6		Uniform distribution	1.0000 149.70 0.7552	1.0000 133.60 0.3895	1.0000 116.74 0.1791	0.9998 109.86 0.08069	0.9995 105.32 0.03805	0.9992 89.55 0.01543	0.9988 78.79 0.007602	0.9985 69.29 0.005074	61.48 0.003861
0.8	1.0000 83.00 0.9259	1.0000 93.13 0.4317	1.0000 84.25 0.1376	0.9997 76.29 0.04540	0.9992 68.73 0.02022	0.9990 65.53 0.01197	0.9982 48.84 0.005796	0.9972 40.51 0.003745	0.9959 34.03 0.003041	0.9943 29.12 0.002722
1.0	1.0000 75.30 0.9526	1.0000 64.42 0.1929	0.9995 57.52 0.04464	0.9987 48.77 0.1700	0.9980 41.44 0.009240	0.9970 35.57 0.006199	0.9944 27.15 0.003906	0.9902 21.58 0.003076	0.9830 17.71 0.002680	0.9709 14.97 0.002402
1.2	1.0000 69.36 0.5920	0.9995 48.16 0.07182	0.9983 38.71 0.01844	0.9967 30.90 0.009036	0.9946 25.38 0.005819	0.9915 21.26 0.004420	0.9801 15.75 0.003134	0.9543 12.64 0.002243	0.9011 11.01 0.001320	0.8085 10.34 0.0005882
1.4	1.0000 47.79 0.2024	0.9983 35.06 0.02504	0.9956 25.81 0.009163	0.9913 19.87 0.005647	0.9835 15.94 0.004010	0.9697 13.39 0.003087	0.9025 10.74 0.001373	0.7428 10.25 0.0003183	0.4973 10.88 0.00003683	0.2428 12.62 0.0000016
1.6	0.9992 39.09 0.03001	0.9955 25.03 0.008900	0.9883 17.22 0.004923	0.9716 13.22 0.003340	0.9338 11.08 0.001971	0.8585 10.25 0.0008686	0.5463 10.75 0.00005315	0.2027 12.90 0.00000079	0.02790 16.85 0.00000001	Not fitted

and reproduction, but that tradeoff should be shown, not imposed. The methods used in the present study can be extended to address this tradeoff (i.e., Mangel and Clark, 1988; Clark and Mangel, 2000), but that is a subject for another study. However, for many overfished stocks that need stock-recruitment relationships for rebuilding analysis, this method is especially appropriate because it indicates the ability of the population to recover from low abundance. For other depleted stocks, use of prior probability distributions based on this method can provide useful information on how quickly the populations could be rebuilt under various management policies.

Acknowledgments

We thank Anand Patil of the University of California Santa Cruz for help in Matlab programming.

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Abstract—To estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught incidentally in regular commercial pelagic longline fishing operations targeting swordfish and tunas, short-duration pop-up satellite archival tags (PSATs) were deployed on captured animals for periods of 5–43 days. Twenty (71.4%) of 28 tags transmitted data at the preprogrammed time, including one tag that separated from the fish shortly after release and was omitted from subsequent analyses. Transmitted data from 17 of 19 tags were consistent with survival of those animals for the duration of the tag deployment. Postrelease survival estimates ranged from 63.0% (assuming all nontransmitting tags were evidence of mortality) to 89.5% (excluding nontransmitting tags from the analysis). These results indicate that white marlin can survive the trauma resulting from interaction with pelagic longline gear, and indicate that current domestic and international management measures requiring the release of live white marlin from this fishery will reduce fishing mortality on the Atlantic-wide stock.

Manuscript submitted 7 March 2005 to the Scientific Editor's Office.

Manuscript approved for publication 6 October 2005 by the Scientific Editor.

Fish. 104:434–444 (2006).

Survival of white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic*

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White marlin (*Tetrapturus albidus* Poey 1860) is an istiophorid billfish species widely distributed in tropical and temperate waters throughout the Atlantic Ocean, including the Caribbean Sea. There is substantial international concern regarding the population levels of this species. The standing committee for research and statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) last assessed the Atlantic-wide stock of white marlin in 2002 and in its continuity-case assessment the committee indicated a total biomass of approximately 12% of that necessary to produce maximum sustainable yield. It was also estimated that the current international fishing mortality level for this species is equivalent to more than eight times the replacement yield, contributing to further decline of the overfished stock (ICCAT, 2005).

Both recreational and commercial fisheries contribute to the mortality of white marlin. A directed recreational fishery exists throughout the tropical and temperate Atlantic (with considerable effort off the coasts of Brazil and Venezuela), as well as off the U.S. mid-Atlantic coast, and there is a growing trend towards catch-and-release practices in all directed recreational billfish fisheries. In contrast to the catches by this directed recreational effort, white marlin are an infrequent bycatch or a retained incidental catch of the international pelagic longline fishery, which targets tunas (*Thunnus* spp.) and swordfish (*Xiphias gladius*). Although white marlin catches in the pelagic longline fishery are relatively rare, the fishery accounts for the majority of the total fishing mortality on this species simply because of the sheer magnitude of pelagic longline effort exerted throughout the Atlantic (ICCAT, 2005).

Both domestic and international management measures are currently in effect for white marlin. The U.S. recreational fishery is managed with a 66″ lower jaw-fork length federal minimum size and a binding ICCAT recommendation that limits the annual U.S. recreational landings to a total of 250 blue marlin (*Makaira nigricans*) and white marlin combined (ICCAT, 2000). U.S. commercial fishermen have been prohibited from landing or possessing white marlin since the implementation of the National Marine Fisheries Service (NMFS) Fishery Management Plan for Atlantic Billfish (NMFS, 1988). ICCAT has responded twice to the decreasing biomass of white marlin and blue marlin by adopting binding

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recommendations requiring reductions in commercial landings by both pelagic longline and purse seine gears (ICCAT, 2000, 2001a). However, these reductions in landings by themselves may ultimately be insufficient to rebuild these two marlin stocks. Goodyear (2002a) found that a reduction of 60% would be necessary to halt the decline of blue marlin, a species which is more abundant, larger, and presumably more robust to the trauma associated with commercial capture (Kerstetter et al., 2003). Given that white marlin are smaller animals, and that the stock is more depleted than that of blue marlin, even more drastic measures are likely necessary to achieve the same management goal for this species.

Because the pelagic longline fishery accounts for the majority of white marlin mortality, understanding the nature of billfish interactions with this gear is critical to developing effective strategies to reduce fishing mortality. Jackson and Farber (1998) reported that 56% of white marlin caught in the Venezuelan longline fishery between 1987 and 1995 were alive at the time of haulback. Data from the U.S. observer program and mandatory pelagic longline logbook records indicate that 71% of white marlin were released alive from U.S. commercial pelagic longline gear between 1996 and 1998 (Cramer[1]). ICCAT has long been encouraging the release of live white marlin through both binding and nonbinding resolutions (ICCAT, 1995, 1996). More recently, the commission has approved binding recommendations that require the release of all live white marlin caught by purse seine and pelagic longline vessels (ICCAT, 1997, 2001b). However, those animals released alive must have a reasonable probability of survival for such management measures to be ultimately effective.

The assessment of postrelease survival presents special problems for large pelagic fishes, which are rarely capable of being held in captivity (de Sylva et al., 2000). In general, recovery rates of billfish tagged with conventional streamer tags by commercial and recreational fishermen have been quite low (0.4–1.83%: Prince et al., 2003; Ortiz et al., 2003). Although this observation is consistent with high postrelease mortality, low recovery rates could also result from tag shedding and from tags that fail to transmit data (Bayley and Prince, 1994; Jones and Prince, 1998). The results of acoustic tracking studies of various billfish species (e.g., striped marlin [*Tetrapturus audax*]: Brill et al., 1993; blue marlin: Block et al., 1992; and black marlin [*Makaira indica*]: Pepperell and Davis, 1999) captured on recreational gear indicate that postrelease survival over periods of a few hours to a few days is relatively high, although mortalities have been observed in short-term tracking studies. Recently, pop-up satellite archival tag (PSAT) technology has proven especially useful to study postrelease survival in several larger istiophorid species, including blue marlin in the Atlantic (Graves et al., 2002; Kerstetter et al., 2003) and striped marlin in the Pacific (Domeier et al., 2003). Only recently have PSATs been attached to smaller (<40 kg) istiophorid billfishes. Horodysky and Graves (2005) used PSATs to evaluate the postrelease survival of white marlin from recreational (rod-and-reel) fishing gear and demonstrated that smaller billfish (≥16 kg estimated weight) can carry PSATs. Their work also suggested high postrelease survival rates in the recreational fishery, especially for fish caught on circle hooks. However, pelagic longline gear presents a different suite of stressors during capture of an animal than does recreational gear. These differences, including long "soak times" (the length of time in each deployment of the gear that the longline is fishing), may also affect postrelease survival rates. In our study, we applied PSAT technology to estimate the short-term mortality of white marlin released alive after capture on pelagic longline gear.

Materials and methods

Fishing operations

White marlin tagging took place off the east coast of Florida (FL), the southwest edge of Georges Bank (GB), the Yucatan Channel (YC), the Windward Passage (WP), and the Mid-Atlantic Bight (MA). These locations are all waters traditionally fished by the U.S. pelagic longline fleet. All tagging operations occurred opportunistically aboard the commercial pelagic longline fishing vessel FV *Carol Ann* (54′ length-over-all) between June 2002 and August 2004. This vessel is typical in size and is equipped for targeting swordfish, mixed swordfish, and tuna within the U.S. coastal pelagic longline fishery. Hook types and sizes were also typical for the fishery and included 7/0 and 9/0 offset J-style hooks (ca. 15° offset; Eagle Claw model no. 9016 or Mustad model no. 7698), 16/0 non-offset circle hooks (Mustad models no. 39660 or no. 39666), and 18/0 non-offset circle hooks (Lindgren-Pitman, Inc., Pompano Beach, FL). Adjusted seasonally, individual leader lengths were 7.5 fathoms (ca. 13.7 m) in the fall northern fishery targeting tuna and 15 fathoms (ca. 27.4 m) in the spring southern fishery for swordfish; this adjustment is standard practice within the fleet (O'Neill[2]). Individual leader lengths comprised a two-fathom "tail" separated from the rest of the leader by a 28-g leaded swivel—a configuration commonly used in this fishery to reduce tangles with other leaders or the mainline. Varying the length of the lines ("buoy drops") connecting the mainline with the small buoy floats on the surface also allows the gear to fish at different depths. Many captains will use two buoy drop lengths in the beginning of a trip to ascertain

[1] Cramer, J. 2000. Species reported caught in the U.S. commercial pelagic longline and gillnet fisheries from 1996–1998. NMFS Sustainable Fisheries Division publication, SFD-99/00-78:1–33. NOAA/NMFS Southeast Fisheries Science Center, SFD, 75 Virginia Beach Dr., Miami, FL 33149.

[2] O'Neill, G. 2003. Personal commun. Carol Ann Sword Corporation. 629 NE 3rd Street, Dania Beach, FL 33004.

the most productive gear configuration. For our study, two buoy drop lengths were used in each set, and these drop lengths were alternated after every 30 hooks: usually 5- and 2.5-fathom (ca. 9.1 and 4.5 m, respectively) lengths in the fall and 10- and 12-fathom (ca. 18.3 and 21.9 m, respectively) lengths in the spring. Electronic hook-timers (Lindgren-Pitman, Inc.; Pompano Beach, FL) were also used during many of the sets to record the time at which an animal was hooked. Bait was usually frozen squid (*Illex* sp.), but occasionally included frozen Atlantic mackerel (*Scomber scombrus*) or a haphazard mixture of the two.

This project consisted of both a pilot and a main study. The pilot study occurred off the east coast of Florida during June 2002 and included deployments of five PTT-100 tags (Microwave Telemetry, Inc.; Columbia, MD) and one PAT (Wildlife Computers; Redmond, WA) tag. The main study was conducted between August 2002 and August 2004 and for this study only PTT-100 HR model tags were used.

Tag models

The physical characteristics of all PSAT tag models used in this study were similar and included a microprocessor, a transmitter, and various environmental sensors, all contained within a resin-filled carbon fiber tube. The tag is made positively buoyant by a spherical glass-bead–embedded float at the base of the antenna. It measures approximately 38 cm in length by 4 cm diameter (including antenna) and weighs between 65 and 75 g (air weight). Tags were rigged with approximately 16 cm of 400-pound test Momoi® brand (Momoi Fishing Co.; Ako City, Japan) monofilament line attached to a large hydroscopic nylon intramuscular tag head according to the method of Graves et al. (2002). The earlier model PTT-100 tags were identical to those used by Graves et al. (2002) and Kerstetter et al. (2003) and recorded one temperature data point for every two-hour period during their five-day (n=3) or 30-day (n=2) deployments, as well as a pre- and postdeployment inclinometer value. The PAT tag recorded environmental data every minute during its 43-day deployment (programmed to disengage from the fish on 30 July 2002) but transmitted data as summary histograms rather than discrete data points. The PAT tag possessed emergency release software as well as a mechanical device (RD-1500; Wildlife Computers, Redmond, WA) for an early emergency release before reaching a depth at which it would be crushed by ambient water pressure (crush depth).

The Microwave Telemetry, Inc. model PTT-100 HR satellite tag was used for the main study and constituted the majority of the PSAT deployments (n=22). This tag has similar physical attributes to those of the model PTT-100 tags previously described, but its functionality was increased by the addition of light and pressure (depth) sensors and an increased data storage capacity. The manufacturer preprogrammed all the PTT-100 HR model tags to detach themselves from the fish after ten days, and the tags were activated prior to attachment to the animal by removing a small magnet from the side of the tag. The tags sampled environmental data at approximately four-minute or two-minute intervals.

White marlin tagging procedures

Preparations for tagging operations were made before each haulback of the gear. Tags were either activated prior to haulback or during haulback immediately following the tagging of a fish and during preparation for tagging another animal. Regardless of the time of external tag activation, all PSATs were allowed to cycle through their full ten-minute computerized internal activation process prior to being attached to a fish. The captain of the vessel identified incoming white marlin on the line during the morning haulback of the gear and fish were evaluated as live or dead based on movement (or lack thereof) alongside the vessel. All live white marlin were tagged, regardless of physical condition.

Fish were manually brought alongside the vessel just aft of the hauling station along the rail and held briefly by the leader until calm. The average distance between the top of the rail and the fish (free-board) on the FV *Carol Ann* was approximately one meter, requiring the use of a tagging pole of approximately 2 m length to reach the fish over the gunwale. The nylon anchor to the PSAT tether was carefully inserted about 5–10 cm below the midpoint of the anterior dorsal fin to a depth of about 5 cm. This location on the fish provides an opportunity for the nylon tag head to pass through the pterygiophore bones without approaching the coelemic cavity (Prince et al., 2002a). For most white marlin in this study (93%), a conventional streamer tag was also attached well posterior to the PSAT.

White marlin were released as soon as possible after tagging by the standard commercial protocol of cutting the leader near the hook unless the hook was readily accessible for manual removal. No animals were resuscitated after tagging. Prior to release, hook type was noted and fish lengths and weights were estimated. Disposition ("live" vs. "dead") and hook location data were collected for all white marlin caught in 2003 and 2004. For the purposes of this study, "internal" hook locations were those in which the barb of the hook was lodged posterior to the esophageal sphincter, and "external" hook locations were noted with more specificity (e.g., "upper jaw"). Hooking on the body away from the mouth ("foul hooking") was considered an "external" hook location. In addition to noting hooking location, a rapid visual examination of each fish was conducted using the five-point "ACESS" scale of activity, color, eye condition, stomach status, and body state (see Kerstetter et al., 2003). The tagging operation, from positive species identification to actual release from the gear, lasted less than 10 minutes. All data, including the time of day, vessel location, and surface water temperature, were recorded immediately after tagging.

Table 1

Summary of locations, trips, and individual sets taken on a commercial pelagic longline vessel between June 2002 and August 2004 during tagging activities. Location refers to National Marine Fisheries Service (NOAA) statistical areas: FEC = Florida East Coast, NEC = Northeast Coastal, MAB = Mid-Atlantic Bight, GOM = Gulf of Mexico, and CAR = Caribbean. For hook type, OS = offset and NOS = non-offset.

	2002		2003	2004	
Months	June	August	July–September	January–February	August
Location	FEC	NEC	MAB	GOM and CAR	MAB
Number tagged	6	2	6	2	12
Sets with tagging	5	1	5	2	3
Bait type	frozen squid	frozen squid	frozen squid	frozen squid, frozen mackerel, or mixture	frozen squid, frozen mackerel, or mixture
Hook type	OS 9/0 J-style and NOS 18/0 circle	OS 9/0 J-style and NOS 16/0 circle	OS 9/0 J-style and NOS 16/0 circle	OS 9/0 J-style and NOS 16/0 circle	NOS 16/0 circle

Data analysis

Survival of tagged animals was inferred from three types of environmental data provided by the tag: water temperature changes, depth changes, and ambient light intensity. Frequent short-scale (<1 hour) variations in both depth and temperature were used as indicators of a live white marlin. The survival of individual fish was also supported by the net displacement, calculated as the distance from the location of the vessel at the time the white marlin was released to that of the first good transmission from the free-floating PSAT to the ARGOS satellite system. The precision of reported location estimates was based on the attitude of the receiving satellite, and transmissions were generated through the ARGOS system (Service Argos, Inc., Largo, MD) and categorized into seven location accuracy codes. Locations were considered "good" for our study if the ARGOS system reported an accuracy code that corresponded to a distance of less than 1000 meters. If a good position was not obtained directly from ARGOS, an average of all location code "0" readings from the first 24-hour period of transmission was used as a proxy location. All distances were calculated with PROGRAM INVERSE (NGS[3]).

Estimates of white marlin postrelease survival were calculated both by including nontransmitting tags as evidence of mortalities and by excluding nontransmitting tags. The 95% confidence intervals associated with these estimates were calculated by using the RELEASE MORTALITY version 1.1.0 software developed by Goodyear (2002b). These confidence intervals were based on 10,000 simulations where underlying postrelease mortality rates derived from the transmitted data were assumed to have no error sources (e.g., no premature releases or tag-induced mortality). For the purpose of these simulations, natural mortality was also assumed to be zero because of the relatively short duration of the tagging deployment period. Unless otherwise noted, all statistical analyses for this study were conducted with SAS version 8.3 (SAS Institute, Cary, NC).

[3] NGS (National Geological Survey). 1975. Version 2.0, modified by M. Ortiz, NOAA/NMFS Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149.

Results

Eight trips (n=112 sets) were taken between June 2002 and August 2004 on the FV *Carol Ann*, a U.S.-registered commercial pelagic longline vessel that operated during the winter and spring in the Caribbean Sea targeting swordfish and during the summer and fall in the mid-Atlantic and Georges Bank region targeting both tuna and swordfish. A summary of these trips and sets is provided in Table 1. Sets were typically made overnight, and gear was deployed at dusk and retrieved at dawn.

Catch rates (catch per 1000 hooks) for target and bycatch species varied by season and location. Swordfish catch rates for retained animals ranged from 1.6 (mid-Atlantic, summer 2005) to 23.9 (Caribbean and Gulf of Mexico, spring 2004). Retained tuna (yellowfin [*Thunnus albacares*]; bigeye, *T. obesus*; and albacore [*T. alalunga*]) catch rates ranged from 0.8 (Caribbean and Gulf of Mexico, spring 2004) to 44.2 (mid-Atlantic, summer 2004). Istiophorid billfishes (blue marlin, white marlin, longbill spearfish [*Tetrapturus pfluegeri*], and sailfish [*Istiophorus platypterus*]) represented approximately 3% of the catch by number, and the overall mean catch rate of white marlin was 1.87 per 1000 hooks. Proportions of white marlin dead at the time of haulback varied among sets, trips, seasons, and locations. The lowest observed proportion dead was 34.4% (mid-Atlantic, summer 2005) and the highest was 50%

Table 2

Summary information for tagged white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic Ocean, June 2002–August 2004. "D/NV" refers to hooks that were deep and not externally visible at the time of tagging. Y=yes; No=no. L=live; PR=premature release; D=dead. —=not available. MSLD=minimum straight line distance (distance between the point where the animal was released and the area where the tag began transmitting data.)

Tag number	Deployment duration	Tag model	Hook type	Hook location	Estimated weight (kg)	Report?	Fate?	% Data	MSLD (nmi/km)
FL-02-01	5-day	PTT-100	18/0 circle	eye socket	18	Y	L	100	42/78
FL-02-02	5-day	PTT-100	9/0 J-style	jaw	27	N	—	—	—
FL-02-03	5-day	PTT-100	9/0 J-style	jaw	20	Y	L	100	26/48
FL-02-04	30-day	PTT-100	18/0 circle	foul	18	Y	PR	n/a	—
FL-02-05	30-day	PTT-100	9/0 J-style	roof	20	N	—	—	—
FL-02-06	43-day	PAT	18/0 circle	eye socket	16	Y	L	33.4	806/1493
GB-02-01	10-day	PTT-100 HR	7/0 J-style	D/NV	20	Y	D	81.5	—
GB-02-02	10-day	PTT-100 HR	16/0 circle	eye socket	23	Y	L	100	109/202
MA-03-01	10-day	PTT-100 HR	9/0 J-style	D/NV	23	N	—	—	—
MA-03-02	10-day	PTT-100 HR	9/0 J-style	eye socket	25	Y	L	85.1	136/252
MA-03-03	10-day	PTT-100 HR	9/0 J-style	jaw	20	Y	L	67.5	80/149
MA-03-04	10-day	PTT-100 HR	16/0 circle	jaw	25	Y	D	57.3	—
MA-03-05	10-day	PTT-100 HR	9/0 J-style	roof	23	N	—	—	—
MA-03-06	10-day	PTT-100 HR	9/0 J-style	roof	25	Y	L	86.1	161/298
YC-04-01	10-day	PTT-100 HR	16/0 circle	jaw	16	N	—	—	—
WP-04-01	10-day	PTT-100 HR	16/0 circle	corner	23	Y	L	100	60/110
MA-04-01	10-day	PTT-100 HR	16/0 circle	eye socket	20	Y	L	44.1	525/973
MA-04-02	10-day	PTT-100 HR	16/0 circle	D/NV	20	N	—	—	—
MA-04-03	10-day	PTT-100 HR	16/0 circle	eye	16	Y	L	16.4	301/557
MA-04-04	10-day	PTT-100 HR	16/0 circle	eye socket	25	Y	L	70.5	632/1170
MA-04-05	10-day	PTT-100 HR	16/0 circle	eye	25	N	—	—	—
MA-04-06	10-day	PTT-100 HR	16/0 circle	eye socket	23	Y	L	22.8	332/615
MA-04-07	10-day	PTT-100 HR	16/0 circle	D/NV	18	N	—	—	—
MA-04-08	10-day	PTT-100 HR	16/0 circle	jaw	14	Y	L	4.4	81/149
MA-04-09	10-day	PTT-100 HR	16/0 circle	jaw	20	Y	L	48.3	436/807
MA-04-10	10-day	PTT-100 HR	16/0 circle	jaw	20	Y	L	17.6	250/463
MA-04-11	10-day	PTT-100 HR	16/0 circle	jaw	23	Y	L	51.0	89/164
MA-04-12	10-day	PTT-100 HR	16/0 circle	jaw	27	Y	L	18.8	255/473

(Caribbean and Gulf of Mexico, spring 2004). The average proportion of white marlin dead at haulback across all seasons and trips was 35.4%.

PSATs were applied to 28 white marlin at the time of haulback. All live white marlin brought to the vessel were tagged regardless of physical condition until the supply of tags available on that trip was exhausted (i.e., if a fish was evaluated as being alive, it was tagged). Estimated weights of tagged fish ranged from 14–27 kg (30–60 pounds) and detailed information for each individual tagged (including hook location, fate, and minimum straight-line distance) is presented in Table 2. Three white marlin tagged with PSATs were caught on leaders attached to electronic hook-time recorders, allowing us to determine the length of time the animal was on the hook before release. Two fish (YC-04-01 and WP-0401) struck the bait in the early morning after local sunrise (7:32 and 8:13 a.m. local time, respectively) and were on the line only for approximately 1.5 hours before release. The third fish (MA-03-01) was caught during haulback at 9:52 p.m. local time on one of the few sets retrieved at night and was hooked for only 11 minutes.

Tag performance

In the pilot study, four of six tags (67%) transmitted archived data as programmed. One tag separated from the fish prematurely several hours after deployment and the data from this tag were omitted from subsequent analyses. For each of the three transmitting early model PTT-100 tags, 100% of the 63 archived data points were received, whereas approximately 33% of the summary data were received from the PAT tag. In the main study,

16 (72.7%) of the 22 PTT-100 HR tags transmitted data to satellites in the ARGOS system as programmed, and an average of 51% (range 4.4–86.1%) of each tag's archived data were transmitted. Two PTT-100 HR tags were found on shore after their transmission period and were returned to us and all the archived data were recovered from each tag.

White marlin survival

Transmitted temperature and depth data from 17 of the 19 functional tags (89.5%) indicated that released white marlin survived for the time periods over which the tags were programmed to collect data. Of the two confirmed mortalities in this study, one fish (GB-02-01) died within one hour after release and sank to the bottom at 145 meters depth. It remained there for approximately 10 hours before the tag and presumably the carcass were scavenged by a shark based on an abrupt change in behavior (depth distribution and movements) and light level (see Kerstetter et al., 2004). The second mortality (MA-03-04) occurred approximately 24 hours following release. After tagging, the animal remained between 0 and 26.9 meters depth before it too was inferred to be the victim of a shark predation event based on similar changes in environmental parameters.

The net displacement of all reporting tags was used as an additional line of evidence to assess postrelease survival of white marlin. All of the tags from putatively surviving animals demonstrated net movements that cannot be explained by surface currents alone. For the 14 surviving fish with PTT-100 HR tags, the average minimum straight-line movement was 246.2 nautical miles (nmi) over the ten-day period, but there was a wide range of net displacement among individuals (80.4–631.5 nmi). Eight of the nine white marlin tagged approximately 350 miles east of Ocean City, Maryland, in summer 2004 moved generally east to northeast, with the exception of one animal that traveled 304.9 nmi to the northwest.

All but one of the tags employed in this study lacked hardware or software that would cause the tag to separate from the fish prematurely if a moribund fish descended below a critical depth. Consequently, nontransmitting tags could result from an animal that died and sank in waters deeper than the pressure capacity of the tags. All eight white marlin tagged with PSATs that did not transmit data were released in or near areas with depths in excess of 2000 meters, the manufacturer's suggested pressure limit for the tags.

The tags that did not transmit data may or may not represented mortalities of the tagged white marlin. These resulting calculated mortality rates therefore depend on whether or not the tags that did not transmit data are included as evidence of mortality. Combining both hook types, the overall mortality rate was 10.5% (95% CI: 0.0–26.3%) if nontransmitting tags were excluded and 37.0% (95% CI: 18.5–55.6%) if nontransmitting tags were included as mortalities.

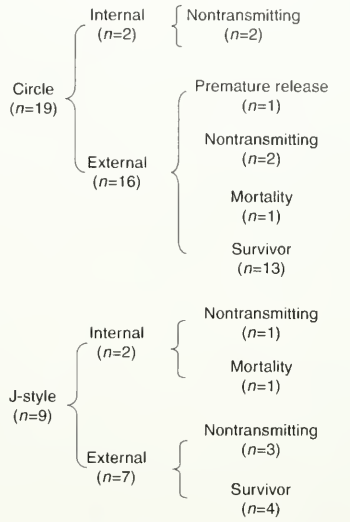

Figure 1

Fate of each white marlin (*Tetrapturus albidus*) tagged with PSAT tags and released from commercial pelagic longline gear in the western North Atlantic Ocean, June 2002–August 2004.

Hook performance

Two general hook types, circle and J-style, were used by the crew of the longline vessel in this study. Nineteen white marlin tagged with PSATs were caught on circle hooks, two of which (10.5%) were lodged internally and 17 of which (89.5%) were lodged externally in the jaw or mouth (Fig. 1). Neither of the two PSATs on animals hooked internally with circle hooks transmitted data. Two PSATs attached to the 17 fish caught with circle hooks lodged externally failed to transmit data, and only one fish caught with a circle hook lodged externally was a confirmed mortality. Nine white marlin tagged with PSATs were caught by J-style hooks. Two fish caught with J-style hooks were hooked internally (22.2%) and seven externally (77.8%). Of the two hooked internally, one tag did not transmit data and the other (fish GB-02-01) was a confirmed mortality. Three of the remaining seven tags on fish caught externally with J-style hooks did not transmit data. Comparisons of hook type and postrelease survival were not significant (Fisher's exact; $P>0.16$). For the 10° offset J-style hooks, the mortality rate was 20.0% excluding nontransmitting tags, and 55.6% if nontransmitting tags were included as mortalities. The 0° offset circle hooks had a 7.1% mortality rate if nontransmitting tags were excluded and 27.7% if

these nontransmitting tags were included as evidence of mortalities.

Nine white marlin were hooked in or near the eye. Seven fish were hooked on either circle or J-style hooks through the eye socket (with no visible damage to the eyeball) and all survived for the 5- or 10-day PSAT deployments. Two PSATs were attached to animals that had been hooked with a circle hook through the eye itself. One PSAT transmitted data consistent with survival, and the other tag did not transmit data. Only one white marlin tagged in this study was foul-hooked, caught in the ventral musculature by a size 18/0 circle hook. The PSAT attached to this fish separated from the fish prematurely.

Discussion

The amount of data archived and transmitted varied greatly among the three models of satellite tags, as well as among the 16 transmitting PTT-100 HRs. The early model PTT-100 tags archived only 63 data points, but 100% of the archived information was transmitted, providing sufficient information to infer survival (Graves et al., 2002; Kerstetter et al., 2003). In contrast, the newer PTT-100 HR tags archived either 4500 or 9145 data points, but not all archived data were transmitted. In this study, most of these tags transmitted a relatively large percentage of the archived data, facilitating determination of the fate of the released white marlin. However, one tag (MA-04-08) had an unusually low data transmitting rate of 4.4%, representing 315 data points over the ten-day tag deployment. Because these data points were transmitted in 11-minute blocks (approximately 9 data points each), they often included complete short-duration movements of a fish from the surface to depth. As the transmitted blocks of data were distributed haphazardly over the entire ten-day tagging period, it remained possible to determine postrelease survival from a high-resolution tag with a low data recovery rate.

Prior studies of postrelease survival have used different lengths of time to ascertain the effects of capture. These have included studies focused on postrelease survival as well as others addressing long-term behavior, movements, and habitat preferences. Graves et al. (2002) justified a five-day deployment period for blue marlin by citing reports of blue marlin recaptured within five days after being released with conventional tags from the recreational fishery, thus demonstrating a return to feeding. Kerstetter et al. (2003) adopted a similar position, although their study on blue marlin also included the deployments of two PSATs for 30 days to evaluate the possibility of delayed mortality. Domeier et al. (2003) used a variety of deployment periods (1–12 month durations) to assess postrelease survival in striped marlin. However, the longer the PSAT deployment period, the more susceptible the animal becomes to both fishing (i.e., recapture) and natural mortality, such as predation, biasing upwards the estimate of postrelease mortality (Goodyear, 2002b).

In our study, we primarily used tags with a ten-day deployment period and believe that this period is sufficiently long to document short-term mortality. Five of seven white marlin mortalities reported in Horodysky and Graves (2005) occurred within the first six hours of release, and the other two died less than three days later. All of the mortalities inferred for the closely related striped marlin by Domeier et al. (2003) occurred within six days of release, and 75% of these mortalities happened in less than two days. The two documented mortalities in the present study (GB-02-01 and MA-03-04) occurred within 24 hours of release.

Direct comparisons of estimates of postrelease survival of billfishes among previous acoustic and PSAT studies are problematic. Many acoustic tracking studies had relatively short observation periods and low sample sizes, and often fish in marginal physical condition were not tagged (reviewed in Domeier et al., 2003). Even among PSAT tagging studies, nontransmitting tags have been addressed with different protocols by various authors. Neither Graves et al. (2002) nor Kerstetter et al. (2003) directly observed mortalities of PSAT-tagged blue marlin. However, in both studies a conservative approach was adopted to estimate postrelease survival by considering nontransmitting tags as representing mortalities; this approach was adopted in part because of a lack of emergency release software or mechanisms on the tags themselves that would release the PSAT prior to its sinking with a dead fish below the depth at which the tag would be crushed. Some new models of satellite tags possess such emergency release software or physical mechanisms, such as glass implosion devices (Domeier et al., 2003) or the RD-1500 metal guillotine from Wildlife Computers (Redmond, WA) that sever the tether of the tag prior to reaching the depth limit of the tag. New generations of tags are also rated to greater crush depths (ca. 2000 m) than earlier models. The PSATs used in our study, with the exception of the one PAT tag, did not possess emergency release software or physical mechanisms. Because all the animals in this study were tagged over or near waters deeper than the crush depths of the tags, any deaths of tagged white marlin could have resulted in the PSATs being destroyed prior to transmitting data while the tag remained attached to the sinking, moribund fish.

There are several reasons why PSATs may not report even with emergency releases, including recovery of the tag by a noncooperative fishing vessel, internal malfunction, or biological activities. Kerstetter et al. (2004) reported on three PSAT tags that were presumably ingested by sharks during predation or scavenging and suggested that a number of nontransmitting tags in all PSAT studies could result from biological activity. Goodyear (2002b) noted that including nontransmitting tags as mortalities would bias mortality estimates upwards if the failure to transmit data was due to causes other than mortality.

The combination of physically more robust tags, emergency release capabilities, and demonstrated mortalities has led authors (e.g., Domeier et al., 2003) to specifi-

cally exclude tags that do not transmit data from subsequent analyses. Because it was not possible to estimate how many such tags in this study could have been due to malfunction versus individual mortality events, we chose to conservatively estimate two postrelease mortality rates: one that includes all nontransmitting tags as mortalities and another that excludes nontransmitting tags. The expensive nature of PSAT technology resulted in relatively small sample sizes and hence large confidence intervals for the estimated postrelease mortality rates. However, as with Horodysky and Graves (2005), simulations with the observed rates in the present study have shown that very large sample sizes (over 200 tags for each hook type) under ideal conditions would be required to reduce these estimates to within ±5% of the true value. The advent of newer tag models with features such as an emergency release will presumably result in lower nontransmitting rates for PSATs and hence more accurate estimates of postrelease survival.

In this study, PSATs attached to some white marlin in marginal physical condition at the time of release returned data consistent with postrelease survival. These included fish MA-04-03, which was hooked through the right eyeball, and fish WP-04-01, which displayed poor, faded color and was moving so little at haulback that it initially appeared dead until careful inspection. Both internal hooking and stomach eversion have been suggested as predictors of subsequent mortality for billfishes (Domeier et al., 2003). Horodysky and Graves (2005) found a 40% mortality rate for internally hooked white marlin, and Domeier et al. (2003) found a 63% mortality rate for similarly hooked striped marlin. We tagged four internally hooked animals, and the one reporting tag (GB-02-01) indicated mortality shortly after release for that fish. Three white marlin with everted stomachs at haulback were tagged in this study, but only one (MA-03-04) remained attached for the duration of the deployment period and transmitted data consistent with mortality. However, the survival of a white marlin (Horodysky and Graves, 2005) and a striped marlin (Holts and Bedford, 1990) with everted stomachs indicates that billfish with everted stomachs can survive if released.

White marlin captured with circle hooks demonstrated a trend of lower postrelease mortality than those hooked with J-style hooks, but this relationship was not significant. This trend in mortality rate versus hook type was independent of whether nontransmitting tags were included as mortalities or excluded from analyses. Horodysky and Graves (2005) observed a significant decrease in mortality for white marlin caught on circle hooks than on J-style hooks (0% versus 35% for J-style hooks). Domeier et al. (2003) also noted a trend for a lower mortality rate among animals hooked with non-offset circle hooks (12.5% versus 29.4% for offset J-style hooks), although this relationship was not significant. The lower mortality-rate trend for white marlin caught by circle hooks than by J-style hooks presented in the present study is also consistent with the results in several other studies of pelagic fishes, such Prince et al. (2002b) for recreationally caught billfish and Skomal et al. (2002) with recreationally caught Atlantic bluefin tuna (*Thunnus thynnus*), which based predictions of postrelease survival on likely injury resulting from specific hooking locations on the animals.

The majority of white marlin caught with circle hooks in the present study were hooked in the mouth or jaw (n=23) rather than internally or by foul hooking on the body (n=5), as was also noted by Horodysky and Graves (2005) for white marlin caught in the directed recreational fishery. In the present study, low numbers of animals caught on either hook types prevented robust comparisons of postrelease survival rates by hook type. More balanced comparisons of postrelease survival among hook types were precluded by both a limited number of expensive PSATs and the imposition of a domestic management measure that prohibited the use of J-style hooks in the U.S. pelagic longline fishery as of 5 August 2004 (FR, 2004). Although beyond the scope of this study, any additional changes in the fishing practices of this fishery, such as the varying lengths of "soak time" between overnight sets (swordfish) and daylight sets (tunas), may also affect the rates of postrelease survival of white marlin.

Ultimately, hooking location may be a more important factor than hook type for predicting postrelease survival. Three of the four PSATs attached to internally hooked animals in this study did not transmit data, although Prince et al. (2002b) reported encapsulated hooks from istiophorid viscera, indicating that internal hooking events are not necessarily fatal. The large percentage of white marlin (35.7%) hooked through the upper lateral palate into the eye or eye socket raises some concern. Istiophorid billfishes are considered to be primarily visual predators (Rivas, 1975) and damage to an eye would be expected to negatively affect the foraging ability of the animal. Billfish are known to have specialized muscle tissue that allows individuals to maintain elevated brain and eye temperatures (Block, 1986), and recent work has revealed color vision in some istiophorids (Fritsches et al., 2003). Dissections of sailfish have revealed that hookings in the eye socket often cause damage to the optic nerve and surrounding ocular musculature (Jolley[4]). The one fish caught with a circle hook through the eye socket in Horodysky and Graves (2005) survived for the entire 10-day deployment period, and in the present study, the seven animals hooked through the eye socket also all survived for their entire deployment periods, as did one white marlin caught with a circle hook through the eyeball. A tagged striped marlin in Domeier et al. (2003) with a punctured eye also survived for ten days, suggesting that this condition is not necessarily fatal over short durations, and healthy swordfish have been observed

[4] Jolley, J. W. 1977. The biology and fishery of Atlantic sailfish *Istiophorus platypterus*, from southeast Florida, 31 p. Fla. Mar. Res. Pub., contribution no. 298. Florida Dep. Natural Resources, Marine Research Laboratory, 100 Eighth Avenue SE, St. Petersburg, FL 33701.

with one healed ocular cavity (D. W. Kerstetter, personal observ.).

We observed a high percentage of hooked white marlin with associated eye damage, specifically in conjunction with circle hooks. In contrast, Horodysky and Graves (2005) noted only one animal out of 40 hooked through the eye with a circle hook. The difference between studies may be a factor of the hook sizes used in the fisheries; the recreational fishery generally uses much smaller circle hooks than the commercial pelagic longline fishery (7/0 and 9/0 sizes versus 16/0 and 18/0). Jolley[4] observed that for 134 (15.8%) of 848 sailfish caught recreationally with J-style hooks, the barbs exited near the eyes, noting that the distal lateral regions of the istiophorid mouth roof (those areas underlying the eyes) are thinly-covered muscle tissue rather than bone. A hook would therefore presumably pass much more easily through this tissue to the eye than if it encountered the lower jaw. Prince et al. (2002b) considered hooking through the upper palate potentially lethal, not only because of the opportunity for the hook to penetrate the occipital orbit, but also because of the tendency for J-style hooks in that location to compromise the integrity of the cranium, making it more susceptible to infection. Two tags that did not transmit data in our study were attached to fish caught with J-style hooks in the center of the upper palate. Borucinska et al. (2002) noted that for blue sharks (*Prionace glauca*) wounded by fishing hooks, an injury caused by a perforating hook may lead to systemic debilitation over longer time intervals than that typically measured with PSAT tags.

The postrelease mortality rates obtained for white marlin from Horodysky and Graves (2005) and this study also allowed the estimation of total U.S. fishing mortality for this species. For the U.S. directed recreational fishery, the white marlin postrelease mortality rate (35% for J-style hooks; Horodysky and Graves, 2005) was applied to estimated yearly catch data and added to "best estimates" of the U.S. recreational landings (Goodyear and Prince, 2003). For the pelagic longline fishery, catch and condition at release data were obtained from the NMFS Pelagic Observer Program database (Lee[5]). The 55.6% postrelease mortality rate (J-style hooks, nontransmitting tags as mortalities; present study) was applied to the number of white marlin released alive to obtain an estimate of the number of fish that died following release. Average underestimates of the actual white marlin fishing mortality to recreational fishery reported landings or to commercial fishery dead discards during this ten-year period were 88.6% and 61.6%, respectively.

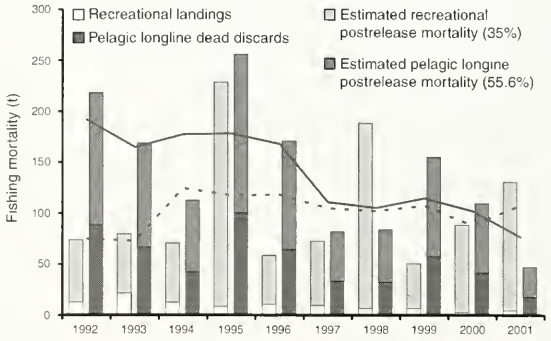

Figure 2

Calculated white marlin (*Tetrapturus albidus*) fishing mortality estimates in metric tons (t) for the recreational and pelagic longline fisheries of the United States. The bottom part of each bar represents the reported mortality in each fishery (recreational landings and commercial dead discards, respectively), while the top part of the bar represents the possible additional fishing mortality based on conservative assumptions of 35% postrelease mortality with J-style hooks for the recreational fishery (Horodysky and Graves, 2005) and 55.6% postrelease mortality with J-style hooks in the commercial pelagic longline fishery (present study). The solid line is the three-year running average for estimated total recreational mortality (reported and estimated postrelease mortality), and the dashed line is the estimated total commercial pelagic longline mortality.

Our analysis indicates that the directed U.S. recreational fishery may generate higher levels of white marlin fishing mortality than the U.S pelagic longline fishery in some years simply due to greater numbers of animals caught (Fig. 2). Because we chose the postrelease mortality estimates based on the historic terminal gear choices of J-style hooks, these results do not account for the probable decrease in total white marlin postrelease mortality resulting from mandated (pelagic longline) and voluntary (recreational) changes in the U.S. fisheries from J-style hooks to circle hooks. However, even this estimated magnitude of actual mortality incurred as the result of the U.S. recreational or pelagic longline fisheries results in the international pelagic longline fishery remaining the largest source of total white marlin fishing mortality in the Atlantic (ICCAT, 2005).

The results of this study clearly demonstrate that white marlin are capable of surviving the trauma associated with capture by pelagic longline fishing gear. Short-term survival of released white marlin was relatively high whether one discounted nontransmitting tags (89.5% survival) or considered nontransmitting

[5] Lee, D. 2004. Personal commun. NOAA/NMFS Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149.

tags to represent mortalities (62.9% survival). These estimates are similar in magnitude to that found for the larger blue marlin released from pelagic longline gear (79% survival; Kerstetter et al., 2003). The documented survival of white marlin indicates that current domestic and international management measures requiring live release from commercial pelagic longline gear will reduce fishing mortality on this species.

Acknowledgments

We thank Captain Greg O'Neill, the crew, and owner Vince Pyle of the FV *Carol Ann* for their field assistance. Andrij Horodysky (VIMS) provided logistical field support, as well as a critical review of the manuscript. Paul Howey, Lissa Werbos, and Shefali Mehta (Microwave Telemetry, Inc.) assisted with the PSAT programming and resulting data. We also thank Eric Prince (NMFS) for his support of the pilot work. This project was funded in part by NOAA/NMFS Cooperative Research Program Grant no. NA03NMF4540420 and the NOAA/NMFS Southeast Fisheries Science Center.

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Application of two methods for determining diet of northern fur seals (*Callorhinus ursinus*)

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Abstract—Examination of hard parts recovered from scats (feces) is currently the most common method for determining the diet of pinnipeds. However, large or sharp prey remains may be spewed (regurgitated) biasing prey composition and size estimations in diet studies based on scats. Percent frequency of occurrence (FO%) and age or size of selected prey remains recovered from northern fur seal (*Callorhinus ursinus*) scat (n=3444) and spew samples (n=267) collected from rookeries on St. George Island and St. Paul Island, Alaska, between 1990 and 2000 were compared to determine if a bias in prey composition and age or size estimations existed between scats and spews.

Overall prey composition was similar between sample type and location, but the relative FO% of primary prey (≥5%) varied by sample type and location. Age or size estimates of walleye pollock (*Theragra chalcogramma*) and of two species of gonatid squids (*Gonatopsis borealis* and *Berryteuthis magister*) were significantly larger in spews than in scats. Observed differences in FO% and estimated age or size of prey species whose remains were found in scats and spews likely result from size-selective digestion of prey remains. Scats were biased toward smaller prey remains, whereas spews were biased toward larger prey remains and cephalopod beaks. The percent overlap between age classes of walleye pollock caught by the commercial trawl fishery and age classes of walleye pollock consumed by northern fur seals varied noticeably between sample types for both islands (scats: St. George=15.5%; St. Paul=4.1%; spews: St. George=94.6%; St. Paul=89.6%). These results demonstrate that the inclusion of multiple sampling methods allows for a more accurate assessment of northern fur seal prey occurrence and prey age and size.

Manuscript submitted 26 October 2004 to the Scientific Editor's Office.

Manuscript approved for publication 12 October 2005 by the Scientific Editor.

Fish. Bull. 104:445–455 (2006).

Pinniped diet analysis involves the identification of prey remains recovered from a variety of sample types. Prey remains are obtained from stomach lavage and enema procedures from feces (scats) and regurgitations (spews), and from stomachs and gastrointestinal tracts. Historically, northern fur seal (*Callorhinus ursinus*) diet studies have relied upon analysis of stomach and intestinal contents collected from scientific takes or harvested animals (Wilke and Kenyon, 1957; Kajimura, 1984; Bigg and Fawcett, 1985; Sinclair et al., 1994) and, more recently, scat samples (Sinclair et al., 1996; Antonelis et al., 1997). Because a thorough analysis of gastrointestinal contents generally requires the sacrifice of an animal, intact gastrointestinal specimens are no longer typically used in diet analyses. Lavage and enema procedures are also not widely used to describe the diet of the population because sample sizes are often small and animals may require chemical immobilization, thereby increasing the risk of injury or fatality (Antonelis et al., 1987; Harvey and Antonelis, 1994).

Presently, scats are the most commonly used sample type in pinniped diet analyses because they are easy to collect, abundant, and noninvasive (Harvey, 1989; Hammond and Prime, 1990). However, many studies have demonstrated the potential biases associated with this sampling method (Jobling and Breiby, 1986; Pierce and Boyle, 1991; Bowen, 2000), including the accumulation of cephalopod beaks in the stomach (Bigg and Fawcett, 1985; Gales et al., 1993; Harvey and Antonelis, 1994) and underestimation of size and frequency of occurrence of some prey species (Bigg and Fawcett, 1985; Harvey, 1989; Tollit et al., 1997). Captive feeding studies of numerous pinniped species have shown that factors such as species, sex, individual activity level, stomach size, gut length, prey digestibility, feeding regime, and meal size affect the degree of erosion and recovery of prey remains in scats (Harvey and Antonelis, 1994; Tollit et al., 1997; Marcus et al., 1998; Bowen, 2000; Orr and Harvey, 2001). Although studies have been conducted to account for these biases through the use of correction factors (Sinclair et al., 1994; Antonelis et al., 1997; Tollit et al., 1997), the different retention and digestive rates of prey remains in the stomach continue to be a leading criticism for diet studies in which scat samples alone are used.

Spews have been analyzed for several species of pinnipeds (Gales et al., 1993; Harvey and Antonelis, 1994; Kiyota et al., 1999; Lowry and Carretta, 1999; Kirkman et al., 2000). Spews contain prey remains such as fish bones, otoliths, and cephalopod beaks. Often these prey remains are too large to pass through the pyloric sphincter and are, therefore, regurgitated from the stomach (Bigg and Fawcett, 1985; Jobling and Breiby, 1986). Although spewings may be found in areas where pinnipeds come ashore, they are often less abundant

than scats (Jobling and Breiby, 1986; Gales et al., 1993) and have largely been excluded from pinniped diet analyses. Spews from northern fur seals are present on summer breeding islands, but diet studies that are based on spews are limited (Kiyota et al., 1999).

Our study is a comparative evaluation of diet based on scat and spew samples collected from northern fur seal breeding rookeries on two islands in the eastern Bering Sea. Prey remains in scat and spew samples were compared for prey species composition, and the age or size of walleye pollock (*Theragra chalcogramma*) and of two species of gonatid squids (*Gonatopsis borealis* and *Berryteuthis magister*) were estimated. Finally, we compared age classes of walleye pollock found in scats and spewings to age classes of walleye pollock caught by the commercial trawl fishery in management regions adjacent to the Pribilof Islands.

Figure 1

Location of St. George Island and St. Paul Island, within the Pribilof Islands, Alaska. Shaded area indicates walleye pollock (*Theragra chalcogramma*) commercial trawl fishery management areas surrounding the Phibilof Islands.

Materials and methods

Sample collection and processing

Scats and spews were collected opportunistically from rookeries on the Pribilof Islands (St. George and St. Paul), Alaska (Fig. 1), during the breeding season between 1990 and 2000. Samples collected from rookeries during this time (late July through September) were considered to be primarily from females of breeding age (Antonelis et al., 1997). Each scat and spew sample was placed in a plastic bag and frozen until it was analyzed in the laboratory. Samples were thawed and soaked in a mild emulsifying soap solution then rinsed through nested sieves of 4.75, 1.4, 1.0, and 0.5-mm mesh. Bones, otoliths, beaks, and eye lenses were recovered from the sieved samples and stored for analysis. Bones, otoliths, and eye lenses were stored dry in vials and beaks were stored in vials containing 50% isopropyl alcohol (Antonelis et al., 1997). Recovered diagnostic fish bones, otoliths, and cephalopod beaks were identified to the lowest possible taxon by comparing them to a reference collection. Distinctions, based on the morphological features of beaks, between some cephalopod species within the family Gonatidae were not possible. Therefore, identifications of four squid species known to occur in northern fur seal diet were categorized into two groups following Sinclair et al. (1994) and Antonelis et al. (1997) and are referred to as Gb-Bm (*Gonatopsis borealis and Berryteuthis magister*) and Gm-Gm (*G. madokai* and *G. middendorfii*). Additionally, distinctions between four gonatid species (*Eogonatus tinro*, *G. berryi*, *G. pyros*, and *G. onyx*), were difficult to determine from the morphological features of beak and, collectively, are referred to as "gonatid group I" in the present study.

Prey indices

Individual prey species and prey groups were analyzed according to their frequency of occurrence (FO) in scats and spews for both islands. The percent frequency of occurrence (FO%) was calculated by dividing the number of scats or spews containing a specific prey species or group by the total number of scats or spews containing identifiable prey remains. Data from each year were pooled for FO% calculations because of low sample sizes in some years. Prey species or groups with a FO% ≥5% when rounded to the nearest integer, for either island or sample type, were considered to be primary prey.

The minimum number of individuals (MNI) of each prey type was calculated for each sample, and summed over all samples. The cephalopod MNI was estimated by using the maximum count of either upper or lower beaks in each sample. Fish MNI was estimated by using the maximum count in each sample from left or right otoliths, plus half of the otoliths for which a side (right or left) could not be determined (Antonelis et al., 1997). Percent MNI (MNI%) was then calculated by

dividing the MNI of each prey species or group (for all samples) by the total MNI of all prey for samples that contained identifiable fish otoliths or cephalopod beaks (or both).

To determine if the occurrence of prey varied by island or sample type (or both), the presence or absence of the primary prey (n=number of scats with prey remains) was modeled as a binomial random variable by using generalized linear models with island, sample type, and the interaction of island and sample type as explanatory variables (S-PLUS 2000, Insightful Corp., Seattle, WA). The interaction was considered significant if adding the interaction significantly reduced the deviance in the model. If the interaction was significant, islands within each sample type or sample types within each island were compared, depending on whether sample type or island reduced more of the overall deviance. If the interaction was not significant, it was removed from the model, and island and sample type effects were tested. Even though data were insufficient to test for differences in prey occurrence between years, year was included in the model as an additive variable.

Comparisons of prey age and size

Recovered walleye pollock otoliths were assigned a condition grade ("good," "fair," or "poor") based on distinctive features such as sulcus definition, shape, chipping, breaks, and wear (Sinclair, 1988). Pollock otoliths of "good" or "fair" condition were measured lengthwise parallel to the sulcus to the nearest 0.1 mm using handheld digital calipers. A correction factor was applied to "fair" otoliths to account for loss of otolith length as a result of digestion (Sinclair, 1988; Antonelis et al., 1997). Fork lengths of prey were estimated by using regression formulae of otolith length against body length (Frost and Lowry, 1981) and age class was estimated from fork-length–age relationships (Sinclair et al., 1994). Pollock otoliths of "poor" condition were enumerated, but not measured, and were not included in prey size comparisons because of their high degree of erosion.

Pollock otoliths recovered from scat samples processed in the early 1990s were measured, but only age class estimations were recorded in the database. Therefore, to test how the size of walleye pollock otoliths varied by sample type and island, otoliths of "good" and "fair" grades were combined into two age categories; juvenile (0–2 age) and adult (3–5+ age) and each sample (scat or spew) was categorized as containing juvenile, adult, or mixed (juvenile and adult) pollock. Multidimensional contingency tables with island, sample type, and age category as variables were used to test interactive effects among variables. A saturated model including all variables and interactions was compared with restricted models by using chi-square goodness-of-fit test (S-PLUS 2000, Insightful Corp., Seattle, WA). Samples were pooled if sample type or island effects were conditionally independent, and two-dimensional contingency tables were then used to test variables that were not independent.

The size range of Gb-Bm consumed by northern fur seals was estimated by measuring the rostral length of lower beaks recovered from scat and spews. Rostral length was measured to the nearest 0.1 mm with an optical micrometer. Because cephalopod beaks are more resistant to digestion and to subsequent loss of length than are otoliths (Sinclair et al., 1996; Tollit et al., 1997), Gb-Bm lower beaks were not assigned condition grades prior to being measured. However, lower beaks showing excessive wear, such as a broken rostral tip, were not measured.

To evaluate Gb-Bm prey size differences between sample type and islands, we developed (using combined samples of both species) regression equations for lower beak rostral length (LRL) against dorsal mantle length (DML) and for DML against weight. Squid specimens were opportunistically collected from commercial pollock trawl fishery bycatch, research driftnets, and NOAA research vessel mid-water trawl operations between 1979 and 2000. Sampling areas were broad ranging throughout the North Pacific, at numerous localities in the eastern Bering Sea, Gulf of Alaska, and subarctic Pacific Ocean south of the western Aleutian Islands (Walker[1]).

The regression of LRL against DML for Gb-Bm was developed by using 757 lower beaks (n=482 Gb, 275 Bm) with a dorsal mantle length range of 21–386 mm and the DML-weight regression was developed by using 1676 lower beaks (n=1048 Gb, 628 Bm) with a dorsal mantle length range of 17–386 mm. The regression included size ranges of Gb-Bm found in northern fur seal scats and spews examined in the present study. Linear models were used to develop regressions of LRL (mm) against DML (mm) and DML against weight (grams):

$$DML = 39.37(LRL) - 0.50.$$

$$\mathrm{Log}(weight) = 2.87\big(\mathrm{Log}(DML)\big) - 4.16.$$

A high degree of correlation (LRL to DML $P<0.001$; $r^2=0.98$; SE=0.51); DML to weight $P<0.001$; $r^2=0.99$; SE=0.01) was found for both regression equations (Walker[1]). Gb-Bm DML data were log transformed and differences in DML between sample types and island were determined by comparing means with a two-sample t-test. Although the DML-weight regression is not used in the analysis, it is included here for future use by other researchers conducting bioenergetics studies.

Prey age or size estimations were limited to walleye pollock and Gb-Bm because sufficient numbers of otoliths or beaks of other primary fish and cephalopod prey species were not recovered from scat and spew samples, or because regressions for the species were unavailable.

[1] Walker, W. A. 2004. NMFS database. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial trawl fishery

Age-class distributions of walleye pollock in scat and spew samples were compared with pollock size-composition data in commercial midwater trawls (National Marine Fisheries Service, North Pacific Groundfish Observer Program). Trawl data included samples collected from August through September 1990 to 2000 in fishery management areas surrounding the Pribilof Islands (Berger[2]; Fig. 1) that encompass northern fur seal foraging habitat (Robson et al., 2004). Walleye pollock fork length from trawls was converted to age class by following the method of Sinclair et al. (1994) for determination of overlap with the age class of pollock consumed by northern fur seals (as estimated from scat and spew samples).

Results

Prey abundance

A total of 1127 scats and 204 spews from St. George Island and 2317 scats and 63 spews from St. Paul Island contained prey remains (Table 1). Prey species composition was similar between scats and spews for each island, but the relative importance of primary prey species based on FO% and MNI% varied by sample type and island (Table 2). Primary prey species (FO% ≥5%) found in both scats and spews consisted of gonatid group I, Gb-Bm, Gm-Gm, northern smoothtongue (*Leuroglossus schmidti*), Pacific herring (*Clupea pallasi*), Pacific salmon (*Oncorhynchus* spp.), Pacific sand lance (*Ammodytes hexapterus*), and walleye pollock (Fig. 2).

Significant interactions between sample type and island were found for Gb-Bm, Gm-Gm, Pacific salmon, and walleye pollock (Table 3); therefore the FO% of these prey was compared within island or sample type. The occurrence of Gb-Bm in scats versus spews from St. George Island was significantly different—spews having a higher FO% than scat. The FO% of Gb-Bm in scats versus spews collected from St. Paul Island was not significantly different. The FO% of walleye pollock was higher for St. George Island scats than for St. George Island spews. Pollock had the highest FO% of all prey in St. Paul Island scat and spews but was not significantly different between sample types. The FO% of Pacific salmon was significantly higher in spews than scat samples for both islands. The FO% of Gm-Gm was significantly higher in St. George Island spews than in St. Paul Island spews. Of the prey for which no interaction between sample type and island was observed, differences in the FO% of gonatid group I, northern smoothtongue, and Pacific sand lance were significant between islands and between sample types (Table 3). Pacific herring was only different between islands. Year of collection had a significant effect on the occurrence of all primary prey species except gonatid group I and was included in the model as an additive variable. Although scat and spew samples were collected during the same season each year, annual comparisons between sample types were not possible because of low sample size within years (Table 1).

Table 1

Numbers of northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska rookeries during the breeding season (late July–September), 1990–2000.

	St. George Island		St. Paul Island	
Year	Scats	Spews	Scats	Spews
1990	162	28	484	1
1991			109	5
1992	84	32	291	13
1993	10	1		
1994	184	46	230	3
1995	149	7	319	17
1996	141	11	337	14
1997	120	35	80	1
1998	199	24	207	5
1999			30	4
2000	78	20	230	
Total (*n*)	1127	204	2317	63

Variations in MNI% were observed between sample types and island for Gb-Bm and walleye pollock (Table 2). The MNI% of Gb-Bm was higher in spews than in scat samples for both islands. Conversely, the MNI% of walleye pollock was higher in scats than in spews for both islands. Scat and spew samples from St. George Island had higher MNI% of Gb-Bm than those collected from St. Paul Island. The MNI% of walleye pollock in both sample types from St. Paul Island was greater than the MNI% of walleye pollock from St. George Island in scats and spews.

Comparisons of prey age and size

A total of 1755 walleye pollock otoliths were recovered from 173 St. George Island scat samples containing walleye pollock and, of these, 1484 were determined to be in "good" or "fair" condition. Of the 152 walleye pollock otoliths recovered from 27 St. George Island spew samples, 105 were graded as "good" or "fair." From St. Paul Island, 17,827 of 20,062 walleye pollock otoliths recovered from 902 scat samples and 154 of 202 walleye pollock otoliths recovered from 23 spew samples were determined to be

[2] Berger, J. 2004. NMFS. database. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Table 2

Percent frequency of occurrence (FO%) and percent minimum number of individuals (MNI%) of prey species recovered in northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. Table only includes prey species with an FO%≥1% within either sample type and on either island.

	St. George Island				St. Paul Island			
	FO%		MNI%		FO%		MNI%	
Prey species	Scats	Spews	Scats	Spews	Scats	Spews	Scats	Spews
Atka mackerel (*Pleurogrammus monopterygius*)	2.1	1.0	<1.0		3.6		<1.0	
Bathylagidae sp.	1.8		<1.0		<1.0		<1.0	
Gb-Bm (*Gonatopsis borealis* and *Berryteuthis magister*)	22.7	55.4	62.5	94.6	5.6	9.5	5.3	32.7
Gm-Gm (*Gonatus madokai* and *Gonatus middendorfii*)	7.4	14.7	2.8	<1.0	9.8	3.2	3.5	1.6
Gonatid group I (*E. tinro*, *G. berryi*, *G. onyx*, and *G. pyros*)	3.9	23.5	1.4	2.1	1.1	4.8	<1.0	2.0
Gonatidae sp.	1.4	1.0	<1.0	<1.0	<1.0		<1.0	
Gonatus sp.	<1.0	2.9	<1.0	<1.0	<1.0		<1.0	
Greenling sp. (*Hexagrammos* sp.)	<1.0				1		<1.0	
Northern lampfish (*Stenobrachius nannochir*)	1.0	<1.0	<1.0		<1.0		<1.0	
Northern smoothtongue (*Leuroglossus schmidti*)	7.4		5.4		1.7		1.5	
Pacific cod (*Gadus macrocephalus*)	<1		<1.0		1		<1.0	
Pacific herring (*Clupea harengus*)	2.0	2.0	<1.0		3.9	4.8	<1.0	
Pacific salmon (*Onchorhynchus* spp.)	14.8	29.4	<1.0		7.5	34.9	<1.0	
Pacific sand lance (*Ammodytes hexapterus*)	2.6		<1.0		8.9		1.1	
Pacific sandfish (*Trichodon trichodon*)	<1.0		<1.0		2	1.6	1.3	
Sablefish (*Anoplopoma fimbria*)	<1.0				1.3			
Unidentifed cephalopod	2.3	4.9	<1.0		1.2		<1.0	
Unidentified fish	27.6	3.9	<1.0		31.2		<1.0	
Unidentified gadid	17.3	15.2	<1.0		33.4	6.3	2.1	
Walleye pollock (*Theragra chalcogramma*)	59.6	36.8	22.9	2.1	71	69.8	82.3	63.3
Sample size (*n*)	(1127)	(204)	(5043)	(5754)	(2317)	(63)	(19,028)	(251)

in "good" or "fair" condition. The occurrence of walleye pollock age classes determined from otolith measurements varied by sample type (Fig. 3).

A multidimensional contingency analysis showed that sample type was independent of island (P=0.087, χ^2=6.26, df=3); therefore data from St. George and St. Paul Islands were pooled to test for differences in age class of prey between sample types. Spews contained a larger percentage of adult pollock (88.0%, P<0.001, χ^2=260.27, df=1) and a smaller percentage of juvenile pollock (9.1%, P<0.001, χ^2=180.91, df=1) than scats. There was not a significant difference in the occurrence of mixed-age pollock between scats (6.4%) and spews (4.0%) (P=0.490, χ^2=0.47, df=1) and only 71 of 1125 (6.3%) samples contained both age classes. A total of 2856 and 5030 Gb-Bm lower beaks were recovered and measured from 225 scat samples and 111 spew samples, respectively, collected at St. George Island (Fig 4.). A total of 719 Gb-Bm lower beaks were recovered and measured from 110 St. Paul Island scat samples and 47 Gb-Bm lower beaks were recovered and measured from five St. Paul Island spew samples. The mean DML of Gb-Bm in St. George Island scat and spew samples was 69 mm (SE=0.10) and 82 mm (SE=0.14), respectively. The mean DML of Gb-Bm in St. Paul Island scat samples was 67 mm (SE=0.21) and in spew samples was 101 mm (SE=6.35). Gb-Bm data were log transformed to meet assumptions of normality for island and sample-type size comparisons. The DML of Gb-Bm estimated from beaks recovered from spew samples was significantly larger than the DML estimated from beaks recovered from scat samples collected from both islands (two-sample t-test, P<0.001 for St. George Island and St. Paul Islands). The DML of Gb-Bm from St. George Island scats was significantly larger than that form St. Paul Island scats (two-sample t-test, P<0.001). In spew samples, estimated Gb-Bm DML was significantly larger on St. Paul Island than on St. George Island (two-sample t-test, P<0.001). However, the number of spews collected from the two islands were highly unequal (n=204, St. George Island; n=63, St. Paul Island).

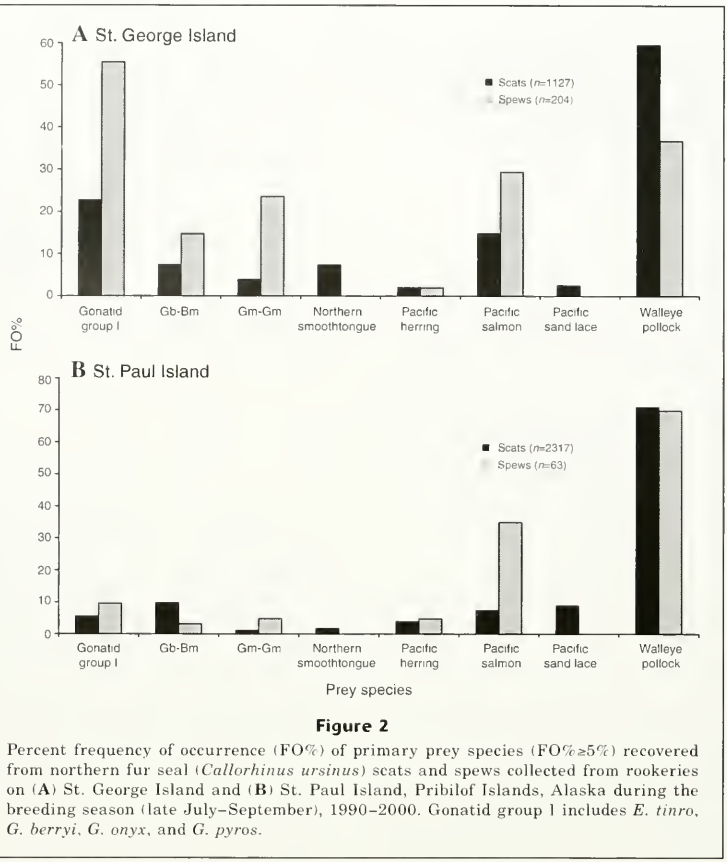

Figure 2

Percent frequency of occurrence (FO%) of primary prey species (FO%≥5%) recovered from northern fur seal (*Callorhinus ursinus*) scats and spews collected from rookeries on (**A**) St. George Island and (**B**) St. Paul Island, Pribilof Islands, Alaska during the breeding season (late July–September), 1990–2000. Gonatid group 1 includes *E. tinro*, *G. berryi*, *G. onyx*, and *G. pyros*.

Overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial trawl fishery

The percent overlap between age classes of walleye pollock caught by the commercial trawl fishery and those consumed by northern fur seals varied between sample types for both islands. Minimal overlap was observed between age classes of pollock found in St. George Island and St. Paul Island scats and those taken by the commercial trawl fishery (St. George Island=15.5%; St. Paul Island=4.1%, Fig. 3). However, the percentage of overlap between age classes of pollock found in St. George Island and St. Paul Island spews and the age classes of pollock taken in commercial trawls was considerable (St. George Island=94.6%; St. Paul Island=89.6%, Fig. 3).

Discussion

Northern fur seal diet studies conducted since the 1980s have primarily used scat samples to determine prey species and size. Despite the presence of spews on rookery and haul-out beaches, only Kiyota et al. (1999) has utilized spews to study northern fur seal diet. Kiyota et al. (1999) examined spews and scats collected from haul-outs (subadult male dominated) and found differences in the prey remains recovered between sample types. We compared the diet of adult female northern fur seals using scats and spews collected from rookeries on the Pribilof Islands over an eleven-year period. We observed differences in the percent frequency of occurrence (Fig. 2) and the estimated age or size (Figs. 3 and 4) of prey between scats and spews. Additionally, the degree of overlap between age classes of walleye pollock consumed by northern fur seals and those caught in

commercial fishery trawls varied considerably by sample type (Fig. 3). These findings highlight the potential limitations of a single sample type, such as scats, and demonstrate that a combination of scat and spew samples can provide a more complete description of northern fur seal diet.

The differences in prey occurrence that were observed among northern fur seal scats and spews in our study may have resulted from the accumulation of irregularly shaped or large prey parts in the stomach (Kiyota et al., 1999). Large cephalopod beaks and fish bones accumulate near the pyloric sphincter and are regurgitated from the stomach, whereas small prey parts pass through the digestive system and are recovered in scats (Bigg and Fawcett, 1985). The different rates of retention of prey parts in northern fur seal stomachs would, therefore, bias scat samples toward small prey species or small bones of large prey species and spew samples toward large prey and cephalopods. For example, the FO% of Pacific salmon, a large boned fish species, was higher in spews than in scats. Kiyota et al. (1999) also observed a higher occurrence of Pacific salmon in spews than in scats of juvenile male northern fur seals from St. Paul Island. The FO% we observed for northern smoothtongue and Pacific sand lance also support a prey species bias between sample types; the small forage fish were among primary prey species found in scat samples but were absent from spew samples.

In addition to differences observed between sample types, we found that the occurrence of primary prey species varied between islands. Specifically, the FO% of gonatid group I, Gb-Bm, Gm-Gm, and walleye pollock varied considerably between sample types and islands, and significant interactions between sample type and island were observed for a number of these species. Walleye pollock was the highest occurring prey in St. George Island scats, but the FO% was significantly lower in spew samples. On St. Paul Island, walleye pollock was the dominant prey species, but the FO% did not differ between scats and spews. Similarly, the FO% of Gb-Bm at St. Paul Island did not differ between sample types. However, the FO% of Gb-Bm was significantly higher in spews than in scats on St. George Island. The FO% of gonatid group I differed both between sample types and between islands; the occurrence of this group was highest in spews, and in samples from St. George Island. Overall, cephalopods occurred at higher frequencies on St. George Island than on St. Paul Island for both sample types. The lone exception was Gm-Gm, which had a lower frequency on St. George Island for scats. Observed differences in cephalopod and walleye pollock occurrence between St. George

Table 3

Results of generalized linear model comparing occurrence of primary prey species identified in northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. The following abbreviations are used for cephalopod prey: Gb-Bm (*Gonatopsis borealis* and *Berryteuthis magister*), Gm-Gm (*Gonatus modokai* and *Gonatus middendorffi*), and gonatid group I (*Eogonatus tinro*, *Gonatus berryi*, *G. onyx*, and *G. pyros*).

	Year			Interaction (island × sample type)			Islands (St. Paul and St. George)			Sample type (scat and spew)			
Prey	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	df	P	
Gb-Bm	47.18	10	<0.0001	4.12	1	0.0424		—		1.95	1	0.1625	St. Paul only
		—			—			—		91.42	1	<0.0001	St. George only
Gm-Gm	118.14	10	<0.0001	8.37	1	0.0038	0.78	1	0.3771 scats only		—		
		—			—		3.84	1	0.0500 spews only		—		
Gonatid group I	17.31	10	0.0678	0.74	1	0.3908	40.12	1	<0.0001	78.10	1	<0.0001	
Northern smoothtongue	70.25	10	<0.0001	0.00	1	0.9862	44.18	1	<0.0001	25.29	1	<0.0001	
Pacific herring	90.37	10	<0.0001	0.03	1	0.8709	6.26	1	0.0124	0.10	1	0.7559	
Pacific salmon	97.94	10	<0.0001	9.70	1	0.0018		—		37.81	1	<0.0001	St. Paul only
		—			—			—		19.59	1	<0.0001	St. George only
Pacific sand lance	57.77	10	<0.0001	0.00	1	0.9887	56.98	1	<0.0001	19.00	1	<0.0001	
Walleye pollock	199.41	10	<0.0001	11.94	1	0.0005		—		0.29	1	0.5921	St. Paul only
		—			—			—		41.46	1	<0.0001	St. George only

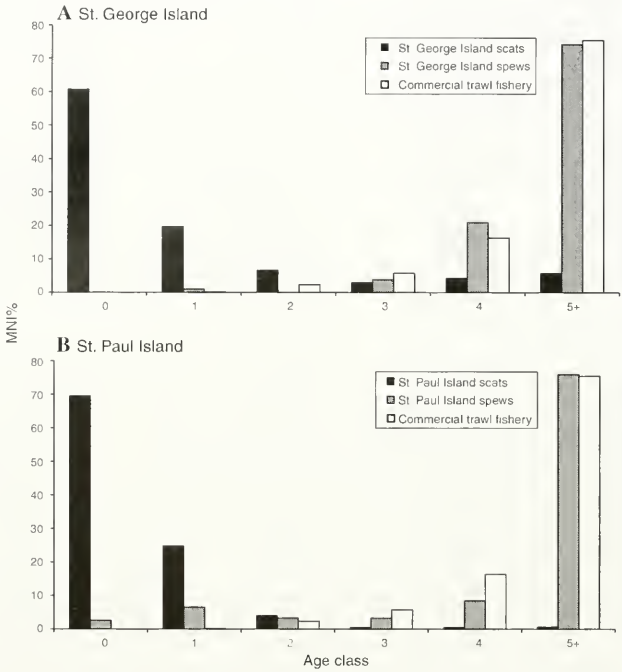

Figure 3

Percent minimum number of individuals (MNI%) of walleye pollock (*Theragra chalcogramma*) age classes recovered from northern fur seal (*Callorhinus ursinus*) scats and spews containing measurable pollock otoliths collected from rookeries on (**A**) St. George Island (1484 otoliths from 173 scat samples; 105 otoliths from 27 spew samples) and (**B**) St. Paul Island (17,827 otoliths from 902 scat samples; 154 otoliths from 23 spew samples), Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. Also shown is the MNI% of walleye pollock age classes caught by the commercial trawl fishery between August and September 1990–2000 in fishery management areas surrounding the Pribilof Islands, Alaska.

Island and St. Paul Island samples are likely related to the availability of prey within reach of female fur seals, which varies according to the physical and biological environment surrounding each island (Sinclair et al., 1994; Antonelis et al., 1997; Robson et al., 2004).

The occurrence of important prey species in scat samples was consistent with previous analyses of northern fur seal scat and stomach samples. However, there were considerable differences in prey occurrence between spews samples and previous studies (Kajimura, 1984; Sinclair et al., 1994, 1996; Antonelis et al., 1997). In northern fur seal diet studies based on analysis of the entire gastrointestinal tract adult females were found to primarily consume juvenile walleye pollock and gonatid squid (Sinclair et al., 1994; 1996). Likewise, diet studies based on scat samples had the highest occurrences of walleye pollock and gonatid squid (Antonelis et al., 1997). Although we observed a similar FO% of walleye pollock in our scat samples, the FO% of gonatid squid and Pacific salmon were significantly higher among spews compared to previous studies based on scat and G.I. tract samples. Thus, it is likely that the importance of some prey species, such as gonatid squids and Pacific salmon, has been underestimated in previous diet studies (e.g., Antonelis et al., 1997).

Significant differences in the size of Gb-Bm were observed between scat and spew samples, demonstrating size-related digestive biases between sample types.

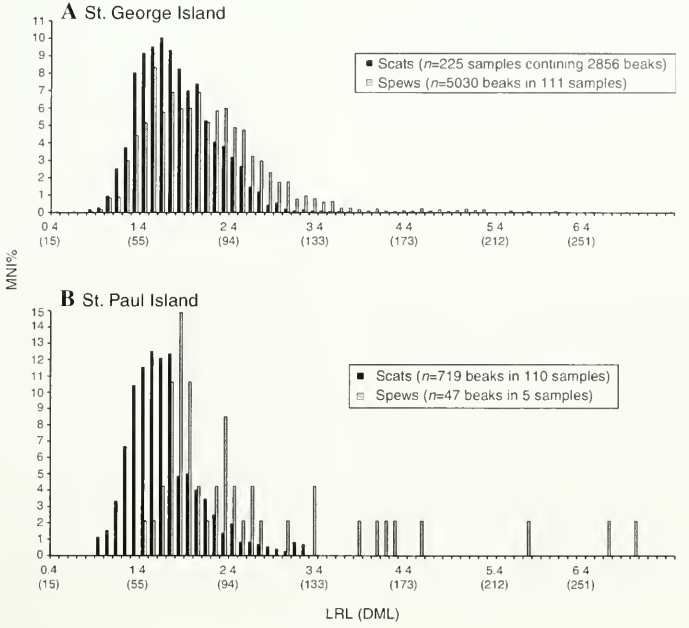

Figure 4

Percent minimum number of individuals (MNI%) of *Gonatopsis borealis* and *Berryteuthis magister* (Gb-Bm) lower rostral length (LRL) and dorsal mantle length (DML) in mm recovered from northern fur seal (*Callorhinus ursinus*) scats and spews containing measurable Gb-Bm beaks collected from rookeries on (**A**) St. George Island and (**B**) St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000.

The dorsal mantle length size of Gb-Bm estimated from lower beaks was significantly larger in spew samples than scat samples (Fig. 4). Digestive biases relating to cephalopod beak size have also been observed in northern fur seal G.I. tracts (Yonezaki et al., 2003), as well as in Australian fur seal (*Arctocephalus pusillus doriferus*; Gales et al., 1993) and California sea lion (*Zalophus californianus*; Lowry and Carretta, 1999) spews and scats. Owing to limited taxonomic resolution of squid species in previous northern fur seal diet studies, direct comparisons of Gb-Bm size were not possible. For instance, Sinclair et al. (1994) presented DML size ranges of beaks recovered from stomachs, but, the cephalopod groups Gb-Bm and Gm-Gm were combined for analysis and were reported as gonatid squid.

We observed a greater percentage of adult walleye pollock in spew than in scat samples (Fig. 3). In addition, few scat and spewing samples were found to contain otoliths from both juvenile and adult age categories, further demonstrating size-related digestive biases of prey remains between sample types. The differences in walleye pollock age classes between scat and spew samples seem to indicate that size estimations of pollock consumed by northern fur seals have likely been underestimated in previous studies using G.I. tracts and scats (Sinclair et al., 1994, 1996). Northern fur seal diet studies based on analysis of the entire G.I. tract have shown that adult females consume primarily juvenile walleye pollock (Sinclair et al., 1994, 1996). However, biases associated with the retention of large prey remains are inherent in studies based on G.I. tract samples (Pierce and Boyle, 1991; Gales et al., 1993), and size-selective relationships between prey otolith size and sample type have been documented for northern fur seals (Kiyota et al., 1999; Yonezaki et al., 2003).

Data that accurately describe the ages of walleye pollock consumed by northern fur seals are critical for assessing potential competition with the commercial trawl fishery, which focuses on adult pollock. Previous northern fur seal diet analyses using scat and G.I tract

samples have revealed that northern fur seals primarily consume juvenile walleye pollock (Sinclair et al., 1994, 1996), indicating that there is limited competition between northern fur seals and the commercial trawl fishery. When walleye pollock age class was estimated from scats collected from 1990 to 2000, we found minimal overlap between the age classes of pollock consumed by northern fur seals and age classes of pollock caught by the commercial fishery during this time (Fig. 3). However, when spew samples were used to estimate age/size of fur seal prey, a high degree of overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial fishery was observed (Fig. 3).

Because of the protective measures that resulted in closures of fisheries in Steller sea lion (*Eumetopias jubatus*) critical habitat, there is concern that fishery pressures in waters surrounding the Pribilof Islands may increase (NMFS[3]). Approximately 75% of the global northern fur seal breeding population inhabits the Pribilof Islands during the summer months (Loughlin et al., 1994) and recent estimates indicate a population decline. The total number of adult males on St. George and St. Paul Islands decreased by 13.4% and 2.8%, respectively, from 2002 to 2003 (Towell et al., 2006; York et al., 2005). Pup production also declined by >5% per year between 1998 and 2002 on both islands (York et al., 2005). At present, the cause of decline is uncertain but there is concern that increased fishing activity in waters surrounding the Pribilof Islands may adversely affect the northern fur seal population. We found that the occurrence and the age or size of some important prey species (such as walleye pollock) has been underestimated in previous northern fur seal diet studies in which only scat samples were used. Because some of these species are also commercially important, northern fur seal conservation and fishery management decisions should incorporate diet-related information acquired from multiple noninvasive sampling methods. This approach would allow better interpretation of northern fur seal dietary requirements, thereby providing a more accurate estimation of the extent to which protective measures in and around the Pribilof Islands should be instituted.

Scat and spew samples were collected simultaneously from the same rookeries on the Pribilof Islands during the breeding season; therefore we do not believe our results were affected by sampling effort. The discrepancies in sample sizes observed in this study may be the result of northern fur seal foraging behavior. Satellite tracking and behavioral studies of female northern fur seals have indicated that individual at-sea foraging trips may range between 6 and 10 days on average (Loughlin et al., 1987; Gentry, 1998; Robson et al., 2004). The accumulation of large cephalopod beaks and fish bones near the pyloric sphincter during this time may have irritated the stomach, causing the fur seals to regurgitate prey remains while at sea prior to their return to the rookeries. Although we do not know the regurgitation rates of fur seals, a tendency to regurgitate food during active digestion would explain the differences in sample size between spew and scat samples found on rookeries of the Pribilof Islands. Differences in proportions of sample types also have been observed on northern fur seal haul-outs (Kiyota et al., 1999), as well as on California sea lion haul-outs (Lowry and Carretta, 1999) and on Australian fur seal rookeries and haul-outs (Gales et al., 1993). Despite the skewed sample sizes between scats and spews in the present study, the observed differences in FO% and estimated age or size of prey between sample types were similar for both islands and were consistent with previous pinniped diet studies comparing scat and spew samples (e.g., Gales et al., 1993, Kiyota et al., 1999).

The various sampling methods used in pinniped diet analyses each have associated biases and sources of error that must be considered. The reliance upon any one sample type in diet assessments will limit one's ability to completely describe prey composition and prey size. Although our results corroborate the findings of previous diet studies with regard to the primary prey consumed by northern fur seals, this study demonstrates that using multiple sampling methods allows for a more accurate assessment of occurrence and age or size of prey.

[3] NMFS (National Marine Fisheries Service). 2001. Steller sea lion protection measures: final supplemental environmental impact statement, 3 volumes. NMFS, NOAA, Alaska Region, P.O. Box 21668, Juneau, AK 99802-1668.

Acknowledgments

We thank W. Walker for assistance with otolith and cephalopod identification, as well as Gb-Bm regression data; J. Thomason and E. Sinclair for help with cephalopod identification; J. Berger for providing commercial trawl fishery catch data; S. Crockford and Pacific Identifications for identification of fish bones; and J. Laake for statistical advice. Reviews and helpful comments on this manuscript were provided by W. Walker, K. Call, T. Loughlin, E. Sinclair, S. Melin, W. Jenkins, and three anonymous reviewers.

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Abundance of adult horseshoe crabs (*Limulus polylphemus*) in Delaware Bay estimated from a bay-wide mark-recapture study

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Abstract—Estimates of the abundance of American horseshoe crabs (*Limulus polyphemus*) are important to determine egg production and to manage populations for the energetic needs of shorebirds that feed on horseshoe crab eggs. In 2003, over 17,500 horseshoe crabs were tagged and released throughout Delaware Bay, and recaptured crabs came from spawning surveys that were conducted during peak spawning. We used two release cohorts to test for a temporary effect of tagging on spawning behavior and we adjusted the number of releases according to relocation rates from a telemetry study. The abundance estimate was 20 million horseshoe crabs (90% confidence interval: 13–28 million), of which 6.25 million (90% CI: 4.0–8.8 million) were females. The combined harvest rate for Delaware, New Jersey, Virginia, and Maryland in 2003 was 4% (90% CI: 3–6%) of the abundance estimate. Over-wintering of adults in Delaware Bay could explain, in part, differences in estimates from ocean-trawl surveys. Based on fecundity of 88,000 eggs per female, egg production was 5.5×10^{11} (90% CI: 3.5×10^{11}, 7.7×10^{11}), but egg availability for shorebirds also depended on overlap between horseshoe crab and shorebird migrations, density-dependent bioturbation, and wave-mediated vertical transport.

Manuscript submitted 29 March 2005 to the Scientific Editor.

Manuscript approved for publication 21 October 2005 by the Scientific Editor.

Fish. Bull. 104:456–464 (2006).

The American horseshoe crab (*Limulus polyphemus*), having persisted largely unaltered for millions of years, is now central to a modern management debate of conflicting interests by commercial watermen, birdwatchers, biopharmaceutical companies, and eco-tourists (Odell et al., 2005). The management controversy is most acute in the Delaware Bay region where the high abundance of horseshoe crabs has resulted in the dependence of migrant shorebirds on horseshoe crab eggs to fuel their northern migration to nesting grounds (Botton and Harrington, 2003).

Because management goals have linked the horseshoe crab fisheries to the viability of other species, such as migrant shorebirds (ASMFC[1]), it is not sufficient to manage on the basis of typical reference points, such as maximum sustainable yield, because sustainable harvest is not the primary issue. In Delaware Bay, the viability of shorebirds has taken precedence in decision making (Botton and Harrington, 2003; Baker et al., 2004). Effective management should reference a critical threshold of horseshoe crab abundance that provides sufficient eggs and should sustain that threshold. Thus, abundance becomes a critical parameter because abundance estimates are useful for predicting the egg biomass that is available to migrant shorebirds and for assessing harvest rate.

Horseshoe crabs bury their eggs in beach sediment, typically 15 to 20 cm deep (Shuster and Sekiguchi, 2003). Eggs are exhumed to the beach surface and become available to foraging shorebirds through a process of entrainment in activated sediment, followed by vertical transport into surface sediments. Nest disturbance, which precedes entrainment of eggs, is predominantly due to bioturbation; whereas wave energy is only a contributing factor because typical estuarine waves do reach nest depth (Jackson et al., 2005). Given a relationship between egg exhumation and spawning density, egg availability could be predicted from current and projected horseshoe crab abundance.

[1] ASMFC (Atlantic States Marine Fisheries Commission). 1998. Interstate fishery management plan for horseshoe crab. Fishery Management Report No. 32, 58 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

Thus, studies to estimate abundance are an important step in the process of managing horseshoe crabs to meet the energetic needs of shorebirds.

We used results from a bay-wide mark-recapture effort during spring 2003 to estimate horseshoe crab abundance. Underlying assumptions of mark-recapture methods were accounted for in our study design and were evaluated during analysis. Recapture effort was distributed over Delaware Bay beaches by involving participants of a bay-wide spawning survey. We related our abundance estimates to reported landings to assess the recent harvest rate and used published fecundity estimates to predict egg production.

Materials and methods

We captured, tagged, and released horseshoe crabs from boats during two periods in 2003: a prespawning-season period (abbreviated to "preseason" in this article) from 26 March to 8 May and a prepeak-spawning period (abbreviated to "prepeak") from 28 to 30 May 2003. The numbers of crabs tagged were 7221 and 10,322 during the preseason period and prepeak period, respectively. The target population was adult horseshoe crabs that were present in Delaware Bay to spawn. One boat fished throughout the bay during the preseason period, and three boats fished nearshore during the prepeak period (Fig. 1). Prepeak period captures took place within strata of equal length along the Delaware Bay shoreline (Fig. 1). During the prepeak period, two boats fished in New Jersey, but only one boat fished in Delaware because of a lack of funding. Because of the additional boat in New Jersey, fishing effort and the number of crabs tagged were higher in New Jersey. Any animal injured during capture was culled and not tagged. Adult males and females were tagged with standard button tags. Tags were 4.4 cm in diameter, bore a unique tag number and carried instructions on the tag for reporting a captured tag. Further detail on tags and tagging methods are described in Brousseau et al. (2004).

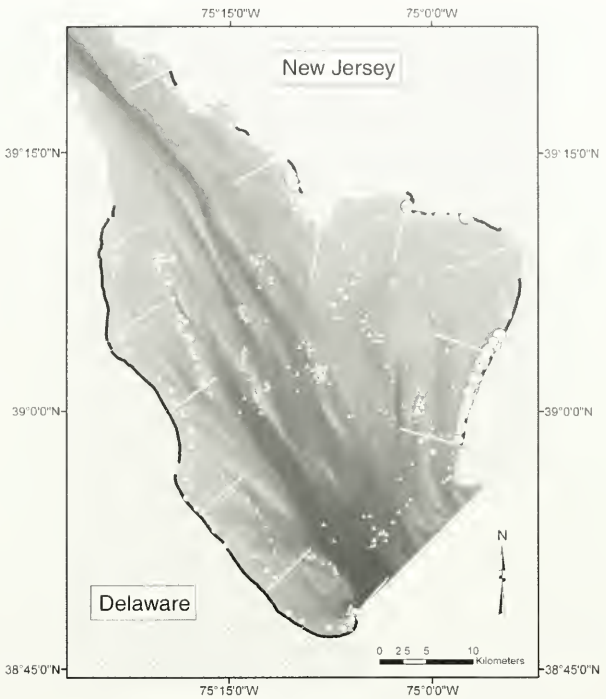

Figure 1

Locations in Delaware Bay where horseshoe crabs (*Limulus polyphemus*) were tagged and released. Size of symbols are graduated to reflect size of catches, and symbol style reflects whether releases occurred during the prespawning season period (26 March to 8 May 2003; triangle) or prepeak-spawning period (28–30 May 2003; circle). White lines perpendicular to the shoreline indicate strata within which catch effort during prepeak-spawning period was equally distributed. Black lines along the shore indicate approximate locations of spawning areas.

Recaptured tags came from the Delaware Bay spawning survey during the peak period of spawning (29 May, 31 May, and 2 June 2003). Although the spawning survey was conducted during spring tides in May and June, the recapture period for abundance estimation was limited to the peak spawning period to help satisfy the assumption of population-closure during the time of mark-recapture study (Borchers et al., 2002). Spawning survey volunteers were instructed to count all horseshoe crabs in sample quadrats and record tags that they encountered inside and outside of the sample quadrats. Flashlights were used when the survey occurred after dark. During the spring tide period around the new moon (29 May to 2 June 2003), 23 beaches were surveyed throughout Delaware Bay (Smith and Bennett[2];

[2] Smith, D. R., and S. Bennett. 2004. Horseshoe crab spawning activity in Delaware Bay: 5 years of a standardized and statistically-robust survey, 10 p. Report to the ASMFC Horseshoe Crab Management Board, Atlantic States Marine Fisheries Commission, Washington DC. Website: http://www.lsc.usgs.gov/aeb/2065/isa%20report%2005.pdf [accessed on 21 October 2005].

Fig. 1). The design of the spawning survey is described in Smith et al. (2002).

Mark-recapture methods

We took two approaches to estimate abundance. The first was an application of Chapman's modification of the Petersen estimator (Borchers et al., 2002). We applied the Petersen estimator separately for each of the two release periods and the three spawning survey dates. In addition, we combined the releases and recaptures for a pooled Petersen estimate.

The second approach was based on an extension of a likelihood presented by Borchers et al. (2002: p. 118, Eq. 6.11). We extended the likelihood to allow for a temporary effect on spawning behavior due to the capture and tagging process by including separate recapture probabilities for each release cohort. The extended likelihood was

$$L_s = \prod_{s=1}^{3} \binom{N - M_{\bullet s}}{u_s} p_s^{u_s} (1-p_s)^{N - M_{\bullet s} - u_s} \binom{M_{1s}}{m_{1s}} p_s^{m_{1s}} (1-p_s)^{M_{1s} - m_{1s}} \binom{M_{2s}}{m_{2s}} (p_s^*)^{m_{2s}} (1-p_s^*)^{M_{2s} - m_{2s}}$$

where N = the abundance at the start of the recapture period at the end of May 2003;

M_{1s} = the number of preseason tagged animals at large at time s;

M_{2s} = the number of prepeak tagged animals at large at time s ($M_{\bullet s} = M_{1s} + M_{2s}$);

m_{1s} and m_{2s} = the recaptures of preseason and prepeak tagged animals at time s;

u_s = the survey count of untagged at time s;

p_s = the capture probability for untagged and preseason tagged animals at time s; and

p_s^* = the capture probability of prepeak tagged animals at time s.

We also fitted a likelihood that set all recapture probabilities to be constant through time, i.e., $p_s = p$ for all recapture surveys, which reduces to Borchers' original likelihood (Borchers et al., 2002: p. 118, Eq. 6.11).

We used maximum likelihood methods to estimate abundance $\hat{N}$ and recapture probabilities ($\hat{p}_s, \hat{p}_s^*$). We used the Petersen estimate for the initial value for $\hat{N}$ and used m_s/M_s as the initial value for recapture probabilities. Profile-likelihood intervals were calculated for the abundance estimates (Borchers et al., 2002). MathCad (vers. 12, Mathsoft Engineering and Education Inc., Cambridge, MA) and SAS (vers. 9, SAS Institute Inc., Cary, NC) were used to find numerical solutions to the likelihood and profile-likelihood equations.

The following assumptions underlie the mark-recapture methods that we applied (Borchers et al., 2002):

1 No emigration or mortality occurred during the period between release and recapture;
2 the tagged animals represented an adequate sample;
3 animals were captured independently of one another;
4 tags were not lost or overlooked; and
5 recapture probability depended only on recapture occasion, was equal among animals of the same sex, and was equal for tagged and untagged animals.

The study was designed through the timing and distribution of releases and recaptures to meet the first two assumptions. The prepeak releases and recaptures were designed to be close in time to meet the assumptions of no emigration and no mortality. Immigration occurred during the time between preseason release and recapture; therefore we estimated the number of adults in Delaware Bay at the time of recapture, which was at the end of May in 2003 (Skalski and Robson, 1992). Some mortality occurred during the time between preseason release and recapture that we were not able to account for; however, we expect that mortality was similar for tagged and untagged animals. We ensured that both initial capture and recaptures were spatially distributed by distributing the releases throughout Delaware Bay during preseason tagging and within strata during prepeak tagging effort (Fig. 1) and by distributing recapture effort systematically by means of the spawning survey (Smith et al., 2002). The third assumption could be violated if horseshoe crabs moved locally in groups. However, recaptures came from widely spaced quadrats, so that even if the animals moved in groups, the whole group was unlikely to be recaptured within single quadrats. Although tag loss could be a significant factor over an extended period, we did not believe that significant tag loss occurred, especially over the five days from prepeak release to recapture period (28 May to 2 June 2003). In a tag-loss study conducted at the United States Geological Survey Leetown Science Center with identical tags, no tag loss over ≥60 days was reported, indicating that tag loss between preseason and recapture periods would not have been significant (Crawford[3]). Tags could have been overlooked during the spawning survey. Females bury themselves in beach sediment during spawning, and their tags could have been readily overlooked. In contrast, males do not bury themselves and the 4.4 cm white button tag is highly visible in daylight or when illuminated by flashlight. Nevertheless, tags on males could have been obscured when the horseshoe crabs piled up during peak spawning. Thus, we restricted our mark-recapture analysis to male horseshoe crabs that were counted and recaptured within 1-m^2 quadrats when surveyors were focusing on a small area.

[3] Crawford, E. 2003. Unpubl. data. USGS-Leetown Science Center, 11649 Leetown Road, Kearneysville, WV 25430

We limited mark-recapture estimates to males because capture probability was not equal for males and females as evidenced by recapture rates. Ratios of males and females captured for the tagging study were used to estimate total abundance with the equation

$$\hat{N} = \hat{N}_m / R_m,$$

where $\hat{N}_m$ = abundance of males; and
R_m = the ratio of males to the total captured.

Abundance of females was estimated by subtraction, i.e., by $\hat{N}_f = \hat{N} - \hat{N}_m$.

We used patterns of recaptures among preseason releases (released from 26 March to 8 May 2003) versus prepeak releases (released from 28 to 30 May 2003) to test the assumption that tagging did not affect spawning behavior. One approach was to use a contingency table analysis that included a comparison of risks of recapture between animals tagged during preseason and prepeak periods. Another approach was based on the extended likelihood presented above (L_s), which included a separate set of recapture probabilities for preseason and prepeak released animals. In this way, the model allowed for a temporary effect on capture probability due to tagging, such as a temporary delay in spawning. We used model comparison techniques (i.e., Akaike's information criteria and likelihood ratio tests) to compare recapture probabilities among preseason and prepeak released animals (Burnham and Anderson, 1998).

Results from a telemetry study conducted in 2004 provided information on spawning behavior of horseshoe crabs caught and released from boats. In 2004, we attached radio transmitters to 60 adult males throughout the Delaware Bay prior to the spawning season. When the animals came on the beach to spawn the signals from the transmitters were recognized by one or more of the 14 fixed station receivers that were arrayed along the shoreline of the bay. In this article, we report the relocation rates (proportion of radio-tagged crabs that were recognized by at least one receiver) from that study because of their relevance to the assumption that tagging does not affect spawning behavior.

An important application of abundance estimates is in the calculation of harvest rates. We calculated harvest rates by dividing estimated abundance into 1) reported landings and 2) projected landings (based on recent regulations). The population that spawns in Delaware Bay disperses widely, some leaving the bay for the ocean. Calculations of harvest rate need to account for these migration patterns because landings from New Jersey and Delaware do not include landings of Delaware Bay spawning animals that were harvested in neighboring states (Virginia and Maryland). However, landings from neighboring states include animals that spawn in embayments other than Delaware Bay. Thus, use of landings from Delaware Bay states alone could underestimate harvest rate and use of landings from Delaware Bay and neighboring states could overestimate harvest rate. To put bounds on the problem, we calculated harvest rate 1) using landings from New Jersey and Delaware and 2) using landings from the Delaware Bay regional states (New Jersey, Delaware, Virginia, and Maryland).

Results

A total of 5398 males and 1823 females were tagged during the preseason period (26 March to 8 May 2003), and 7091 males and 3231 females were tagged during the prepeak period (28 to 30 May 2003; Table 1). Animals that were injured during capture were culled and not tagged. Culling rates were 0.19 during the preseason period, 0.05 during the prepeak period, and 0.12 overall.

During the spawning survey 22,051 males and 6675 females were counted in quadrats and examined for tags. Forty-eight tagged animals were recaptured during the spawning season surveys conducted 29 May, 31 May, and 2 June 2003. Nineteen of the recaptures were within quadrats, and 29 were between quadrats. Only three of the recaptured tags were from females. This number is not surprising; tags are difficult to detect on females because the females remain buried during spawning. The between-quadrat recaptures were not used in the estimation because we did not have a corresponding count of unmarked animals.

Using the Petersen estimator and all releases, we estimated that there were approximately 14.5 million (SE=3.2 million) adult male horseshoe crabs in Delaware Bay during peak spawning at the end of May 2003. Using just the prepeak releases, we estimated 13 million adult males (SE=3.6 million).

Model comparisons indicated that recapture probabilities were time-specific, but the temporary effect on recapture probabilities was not supported by the data (Table 2). The maximum likelihood estimate of male abundance with model 2 (Table 2) was 16.1 million (90% CI: 9.9 to 22.3 million). The difference between the Petersen estimate and the maximum likelihood estimate could have been due to model 2 that allowed for time-specific recapture probabilities, whereas the Petersen estimator did not. The maximum likelihood estimate based on constant recapture probabilities (i.e., model 1 in Table 2), matched the Petersen estimate (14.7 million for model 1 and 14.5 million for the Petersen estimate).

Sex ratios were different for the preseason and prepeak spawning periods in a pattern consistent with a sex-specific migration schedule. There was a smaller proportion of adult females in the bay during the preseason period (0.25) than when spawning activity was near its peak (0.31), which is consistent with the known observation that males migrate earlier than females. Sex ratios observed during the prepeak period were used to estimate abundance in the bay during the peak spawning period.

The assumption of equal catchability of tagged and untagged animals is an important assumption that af-

Table 1

Mark-recapture statistics for tagged horseshoe crabs (*Limulus polyphemus*) released during a prespawning season period (26 March to 8 May 2003) and a prepeak-spawning period (28 to 30 May 2003) and recaptured during spawning surveys on 29 May, 31 May, and 2 June 2003. M_{1s} is the number tagged preseason and M_{2s} is the number tagged before the peak at the time of the survey date (i.e., occasion s); u_s is the number of untagged that were counted during the survey; and m_{1s} is the number of prespawning season crabs recaptured and m_{2s} is the number of prepeak-spawning period crabs recaptured during the survey. Number untagged along the survey portion of the beach (u_s) was estimated from quadrat counts, i.e., [*number untagged on beach* = *beach length* (m) × *mean number per quadrat* (no./m^{-2}) – *number recaptured on beach*]. Survey portion of the beach was less than 1 km.

						Along beach			Quadrats		
Sex	Location	s	Survey date	M_1	M_2	u_s^+	m_{1s}	m_{2s}	u	m_{1s}	m_{2s}
Males	Baywide	1	29 May	5398	4828	55,750	3	4	6846	1	2
		2	31 May	5398	7091	48,498	10	6	5117	2	1
		3	2 June	5398	7091	96,718	10	12	10,088	4	8
	New Jersey	1	29 May	1448	3703	25,123	0	4	3890	0	2
		2	31 May	1448	5254	16,376	3	6	2113	1	1
		3	2 June	1448	5254	29,630	0	9	3524	0	6
	Delaware	1	29 May	3950	1132	30,631	2	0	2956	1	0
		2	31 May	3950	1837	32,129	7	0	3004	1	0
		3	2 June	3950	1837	67,099	10	3	6564	4	2
Females	Baywide	1	29 May	1823	2143	18,224	0	0	2149	0	0
		2	31 May	1823	3231	17,022	1	1	1712	0	0
		3	2 June	1823	3231	27,339	0	1	2814	0	1
	New Jersey	1	29 May	488	1567	8021	0	0	1169	0	0
		2	31 May	488	2268	3993	0	1	532	0	0
		3	2 June	488	2268	6859	0	0	809	0	0
	Delaware	1	29 May	1335	576	10,202	0	0	980	0	0
		2	31 May	1335	963	13,029	1	0	1180	0	0
		3	2 June	1335	963	26,480	0	1	2005	0	1

Table 2

Comparison between three likelihood-based models for mark and recapture of horseshoe crabs (*Limulus polyphemus*). Each model allowed a differed pattern of variation in recapture probabilities. The models are listed in order from least to most complex. In model 1, the recapture probabilities were set to be constant for both release cohorts (prespawning season period and prepeak-spawning period) and for all three recapture occasions. Model 2 allowed recapture probabilities to be time-specific, but equal for release cohorts. Model 3 allowed recapture to be time and cohort specific. Lower values for Akaikie information criteria (AIC) and ΔAIC indicate a better model fit; ΔAIC = 0 is the best fitting model. Likelihood ratio test (LRT) compares two nested models, and a significant P-value indicates the more complex model is supported.

				Likelihood ratio test	
Model	Variation in recapture probabilities	AIC	ΔAIC	Models compared	P-value
1	Constant	−348512.08	1713	Models 1 and 2	<0.0001
2	Time-specific	−350225.72	0	Models 2 and 3	0.77
3	Time and cohort-specific	−350220.83	5		

fects the accuracy of abundance estimates. Therefore, it was important to evaluate thoroughly whether tagged animals had different catchability than untagged animals. We tested for a temporary delay in spawning by comparing relative risk of recapture among the two release periods and by fitting a likelihood model that incorporated separate recapture probabilities for each release cohort (Table 2). Evidence did not support the hypothesis that initial capture and tagging temporarily affected spawning behavior (χ^2=2.03, df =2, P=0.36). The difference between the two release periods in the risk of being recaptured during peak spawning was

Table 3

Maximum likelihood estimates of abundance for adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay during the end of May 2003. Estimates of females and for both sexes combined ("Total") are based on mark-recapture estimates of males and sex ratios among the animals caught and released for this study. Adjusted estimates take into account the possible effect of capture on spawning by reducing releases of males by 0.88, which is an observed relocation rate for radio-tagged males.

	Maximum likelihood estimates		Adjusted estimates based on relocation rates from radio-tagged males	
	Abundance	90% CI	Abundance	90% CI
Males	16,140,000	9,910,000–22,300,000	13,730,000	8,780,000–19,400,000
Females	7,350,000	4,520,000–10,160,000	6,250,000	4,000,000–8,840,000
Total	23,490,000	14,430,000–32,460,000	19,980,000	12,7800,000–28,240,000

0.001 (90%CI: −0.0007 to 0.003). A model comparison test (likelihood ratio test in Table 2) did not support cohort-specific recapture probabilities (P=0.77). Although the difference in relative risk was in the direction of a temporary delay in spawning, the difference in recapture probabilities tended to be in the opposite direction. On two out of the three recapture occasions, the prepeak release cohort had a higher recapture probability than the preseason cohort. The maximum likelihood estimate of abundance of males with the use of model 2 (Table 2) was 20% higher for all releases (16.1 million crabs) than for prepeak releases only (13.4 million). A temporary delay in spawning would tend to cause abundance estimates based on late-releases to be higher than estimates including early releases, but in fact the opposite occurred. Thus, based on three lines of evidence, it is unlikely that there was a temporary delay in spawning due to the capture and tagging of males.

Another way in which tagged animals may behave differently from untagged animals is that tagged animals may forego spawning altogether. In 2004, we radio tagged horseshoe crabs using the same capture process that was used to tag animals in 2003. The radio-tagged horseshoe crabs were detected by radio receivers at high tide when the radio-tagged crabs emerged from the water to spawn. An array of fixed station receivers ensured nearly complete coverage of spawning habitat in Delaware Bay. Among radio-tagged males, we observed that age-specific relocation rates were 0.44, 1.00, and 0.74 for young, middle, and old-aged males, respectively. The frequencies of these age groups in the end of May 2003 tag releases were 0.07, 0.62, 0.31 for young, middle, and old-aged males. Thus, the average relocation rate predicted for the 2003 releases would be 0.88 (i.e., $0.44\times0.07+1\times0.62+0.74\times0.31=0.88$). There are several reasons for a failure to detect radio-tagged animals, namely behavioral response, movement beyond the range of radio receivers, transmitter loss or failure, and animal mortality. It is also possible that some adults migrate but do not spawn in a given year. Nevertheless, to be conservative, we adjusted the tag releases by the observed relocation rate (0.88) and computed estimates using the reduced releases. The 12% reduction in releases resulted in a 15% reduction in the abundance estimates (Table 3). From currently available estimates of fecundity (88,000 eggs per female; Shuster and Botton, 1985), we estimated that egg production in 2003 was 5.5×10^{11} (90% CI: 3.5×10^{11} to 7.7×10^{11}).

The adjusted estimates of abundance were 13.7 million (90% CI: 8.8 to 19.4 million) for males and 6.25 million (90% CI: 4.0–8.8 million) for females (Table 3). Landings in New Jersey and Delaware during 2003 were 2.4% (90% CI: 2–4%) of abundance estimates (Table 4). When landings from Virginia and Maryland are included, landings during 2003 were 4% (90% CI: 3–6%) of abundance. Harvest rates were similar for males and females because the sex ratio in the landings was similar to the ratio observed in our fishery-independent catch. We believe that our fishery-independent catch was a representative sample of mature animals in the bay.

We caught horseshoe crabs prior to and during the spawning migration. Thus, a comparison of pre- and postmigration catches could indicate the proportion of the population that over-wintered in the bay. We caught, on average, 18 adults per 15-min. tow on a vessel with two 2.3-m dredges from 25 March to 3 April 2003 prior to the spawning migration, which appeared to begin in mid-April. The catch-per-tow was 39 adults per tow during the period from 13 April to 8 May 2003 and 60 adults per tow during 28 to 30 May 2003. Thus, we were catching approximately one third (18/60=0.3) of the animals prior to spawning migration; this fraction could represent the proportion of the population that over-wintered in the bay and that did not migrate to the ocean between 2002 and 2003.

Discussion

There have been few attempts to estimate abundance of adult horseshoe crabs in Delaware Bay during the spawning run when the population is spatially concentrated. Shuster and Botton (1985) estimated population size from surveys on Delaware Bay beaches. However, a large portion of the bay was not included in the target

Table 4

Harvest rates calculated from 2003 landings and abundance estimates of adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay at the end of May 2003. To be conservative, estimates were adjusted according to the observed relocation rate (0.88) for radio-tagged male animals (see Table 3). NJ=New Jersey; DE=Delaware; VA=Virginia; and MD=Maryland.

	Delaware Bay (NJ and DE)			Delaware Bay Region (NJ,DE,VA,MD)
	Males	Females	Total	Total
Landings[1]	318,400	151,900	470,300	745,800
Abundance	13,700,000	6,250,000	19,980,000	19,980,000
	8.8 to 19 mil	4.0 to 8.8 mil	12.8 to 28 mil	12.8 to 28 mil
Harvest rate	0.023	0.024	0.024	0.04
	0.02 to 0.04	0.02 to 0.04	0.02 to 0.04	0.03 to 0.06

[1] ASMFC (Atlantic States Marine Fisheries Commission). 2004. 2003 Review of the fishery management plan for horseshoe crab (*Limulus polyphemus*), 13 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, D.C. 20005

population study and was excluded from the survey. Carmichael et al. (2003) used transects located on a grid and visual counts in a shallow clear-water estuary to estimate abundance of the population in Pleasant Bay, Cape Cod, Massachusetts. Other estimates of the Delaware Bay population have been based on offshore surveys during nonspawning periods when populations are dispersed and possibly mixed (Botton and Haskin, 1984; Botton and Ropes, 1987; Hata and Berkson, 2003). Our mark-recapture estimates apply to adult horseshoe crabs present in Delaware Bay during late May 2003 when spawning peaked.

In previous horseshoe crab population estimates that were based on offshore surveys (Botton and Haskin, 1984; Botton and Ropes, 1987; Hata and Berkson, 2003), capture efficiency was unknown, and adults that remained in estuaries (i.e., those that did not migrate to the ocean after spawning) were not sampled. Hata and Berkson (2003) concluded that the capture efficiency for their trawl survey was intermediate between that of the trawl survey reported in Botton and Haskin (1984) and that of the hydraulic dredge survey reported in Botton and Ropes (1987). The most recent estimate of offshore abundance of 7.1 million crabs was reported by Hata and Berkson (2003). Botton and Haskin (1984) reported densities that were 1.8 to 2.9 times the densities reported by Hata and Berkson (2003), which would indicate a population estimate of 12 to 20 million according to the data of Botton and Haskin (1984). Botton and Ropes (1987) reported a minimum population of 2.3 to 4.1 million. The proportion of adults that remain in the Delaware Bay and do not migrate to the continental shelf after spawning is unknown. However, if the proportion of nonmigratory adults is sizeable (e.g., on the order of 0.3, which was indicated by our fishery-independent catches) then that, along with gear inefficiencies in trawl surveys, could explain the difference between the estimates in our present study and those of Hata and Berkson (2003).

Bias due to assumption violation is another reason for differences in estimates. We designed our study to obtain a representative sample when horseshoe crabs were concentrated and to minimize the time between release and recapture periods so that only a few days separated the prepeak release and recapture occasions. We released 17,543 tagged horseshoe crabs over two periods and examined 28,738 horseshoe crabs for tags, counting them in quadrats during subsequent spawning surveys (29 May, 31 May, and 2 June 2003). Low recapture rates (<1%) were consistent with a large population. However, it was important to evaluate the potential effects of assumption violations. Tag loss and tag-induced mortality were likely to be trivial because of the short period during which crabs were at large and results from field studies and laboratory experiments have shown no tag loss or tag-induced mortality (Crawford[3]; Brousseau et al., 2004). Brousseau et al. (2004) attached combined acoustic and radio tags and standard button tags to 24 female horseshoe crabs along two beaches in Delaware Bay, and then tracked them for eight days. All 24 were detected at least once, and 20 spawned on the beach of release within eight days of release, indicating that handling and tagging had a minimal effect on spawning behavior. Tags could have been overlooked during the spawning survey, which is why we limited our analysis to males counted and recaptured within 1-m^2 quadrats.

We evaluated the effect of capture and tagging on spawning behavior, and found no evidence that tagged males delayed spawning. Using radio-tagged horseshoe crabs, we believe it is possible that tagged crabs terminated spawning, and we adjusted abundance estimates based on relocation rates of radio-tagged crabs. Thus, we based our inference on abundance estimates that were adjusted downward to account for that possibility.

Recapture rates were low over the short time period for our study. However, annual recapture rate was approximately 4% for all tag releases and recaptures.

Mark-recapture studies have been frequently applied to marine species for describing migration or estimating mortality (Hoenig et al., 1998; Bacheler et al., 2005). Mark-recapture methods are used infrequently for abundance estimates of marine species, with the exception of anadromous species, whose spawning migration concentrates the population and enhances opportunities for recapture (Schwarz and Taylor, 1998). Similarly, the unusual horseshoe crab spawning migration and behavior concentrated the population and made them assessable for recapture. The validity of our abundance estimates is founded on a large number of tag releases and animals checked for tags, a study design that ensured population closure, an adequate number of samples to represent the population, and an evaluation of the underlying assumptions.

The sex ratio in our fishery-independent catch (69% M: 31% F), which we believe is a representative sample of adults in the bay at the time of peak spawning, was similar to the sex ratio in the landings (68% M: 32% F). Hata and Berkson (2003) observed a similar sex ratio among adults in an offshore trawl survey (63% M: 37% F). Although, commercial landings in 2003 were not skewed toward the harvest of females, harvest could have selected females disproportionately in past years.

The horseshoe crab harvest has been reduced through a series of reductions mandated by ASMFC (ASMFC[4]). Although there is evidence of stock decline coincident with increased landings in the past 10–20 years (ASMFC[4]), the estimates presented in the present study indicate recent regulatory changes had achieved a low harvest level by 2003. Based on the abundance estimates reported here, harvest rate in 2003 was 0.024 (90% CI: 0.02 to 0.04) for Delaware Bay state landings and 0.04 (90% CI: 0.03 to 0.06) for Delaware Bay area landings. In 2004, additional regulations were enacted, which capped landings at 150,000 per state for Delaware and New Jersey and prohibited harvest during May and early June when migrant shorebirds stopover in Delaware Bay. As a result of the 2004 regulations, landings dropped to 173,023 (males and females) for Delaware and New Jersey combined, which is a 63% drop from 2003 landings. Sex ratio of the 2004 landings was 68% M: 32% F, consistent with the 2003 landings.

Estimating abundance is an important step in the process of determining the current capacity for horseshoe crab egg production in the bay and for managing for the energetic needs of shorebirds. We estimate that egg production in 2003 was 5.5×10^{11} (90% CI: 3.5×10^{11} to 7.7×10^{11}). The U. S. Fish and Wildlife Service Shorebird Technical Committee (USFWS[5]) estimated that a population of 423,000 shorebirds would require 1.07×10^{11} horseshoe crab eggs as they migrated through Delaware Bay. This represents approximately 20% of all egg production, which would have to be available temporally and spatially during the shorebird migration.

Egg availability for shorebirds will depend also on overlap between horseshoe crab and shorebird migrations, density-dependent bioturbation, and wave-mediated vertical transport. Some important aspects of egg production and the process of making eggs available to foraging shorebirds are not well understood and have not been quantified. For example, if fecundity is found to be age- or size-related, then age or size would need to be incorporated in a calculation of egg abundance. Also, the process of bioturbation, which releases buried eggs to the beach surface, is known to be related to the density of spawning females, but has not been parameterized (Jackson et al., 2002). Determination of the dietary requirements of migrant shorebirds in terms of horseshoe crab eggs coupled with reliable estimates of abundance, fecundity, and bioturbation rates, will set the stage for a management of horseshoe crabs that takes into account the trophic support it provides in Delaware Bay.

[4] ASMFC (Atlantic States Marine Fisheries Commission). 2004. Horseshoe crab 2004 stock assessment report, 87 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[5] USFWS (United States Fish and Wildlife Service). 2003. Delaware Bay shorebird-horseshoe crab assessment report and peer review. U.S. Fish and Wildlife Service Migratory Bird Publication R9-03/02, 99 p. USFWS, 4401 N. Fairfax Drive, Arlington, VA 22203.

Acknowledgments

We thank many individuals involved in the tagging study and the Delaware Bay spawning survey. Principal among them were Stewart Michels, Lorne Brousseau, Mike Oates, Bruce Freeman, Carl Shuster, Susan Love, staff from the DE Coastal Program and the Delaware National Estuarine Research Reserve (DNERR), Benjie Swan, Bill Hall, Glenn Gauvry, Sherry Bennett, and representatives from Audubon, The Nature Conservancy, the Slaughter Beach folks, and the USFWS. Funding came from the USGS, NJ FG&W, and Delaware Department of Natural Resources and Environmental Control (DNREC). We appreciate comments from Stewart Michels, Greg Breese, and John Young on an early draft of the paper.

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Estimates of commercial longline selectivity for Pacific halibut (*Hippoglossus stenolepis*) from multiple marking experiments

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The term "selectivity" refers to the relationship between the size (or age) of a fish and its vulnerability to a given kind of fishing gear. A selectivity schedule, along with other parameters, is normally estimated in the course of fitting a stock assessment model, and the estimated schedule can have a large effect on both the estimate of present stock abundance and the choice of an appropriate harvest rate. The form of the relationship is usually not known and not well determined by the data, and equally good model fits can often be obtained with different plausible specifications of selectivity. Choosing among the model fits and associated abundance estimates in this situation is problematic (Sigler, 1999; Sullivan et al., 1999).

The selectivities of different gears can be compared by fishing the gears side by side, but without knowing the size composition of the stock being fished, it is impossible to determine the form of the selectivity functions. Therefore, one has to make some assumptions about them in order to locate estimates (Millar and Fryer, 1999, and references therein). In this case, too, equally good fits can often be obtained with a variety of assumed forms (Huse et al., 2000; Woll et al., 2001); therefore the true form cannot be determined by simple fishing experiments.

Mark-recapture data can yield direct and reliable estimates of selectivity because in this situation the size composition of the fished stock is known (Myers and Hoenig, 1997). In this note, we report estimates of the commercial longline selectivity of Pacific halibut (*Hippoglossus stenolepis*) based on the large number of mark-recapture experiments conducted by the International Pacific Halibut Commission (IPHC) in the 1960s, 1970s, and 1980s. A similar analysis was done by Myhre (1969), but he used data from only two experiments; the present study uses data from more than 100 experiments.

Materials and methods

Kaimmer (2000) described all IPHC tag data for all varieties of external tags in setline and trawl catches dating back to 1925. We also used tag data for all varieties of tags (except the small strap type); however, our data were for tags released during setline catches only and our data dated back to 1960, the first year of recorded data in the computer release and recovery IPHC database. The total number of tags released was over 100,000, of which more than 13,000 were recovered in the commercial longline fishery. About half of the releases were at systematically placed setline survey stations that covered a large part of an IPHC regulatory area (Fig. 1). The other half were at "spot" fishing locations, deliberately chosen to produce good catches, either for marking or for gathering data on the performance of different gear types. For our study, an experiment was defined as all releases of a given tag type in a given regulatory area in a given year during either survey or spot fishing operations (not both), where at least 10 fish were released. Between 1960 and 1990 there were 131 such experiments.

These data are not usable for estimating exploitation rates or migration rates because of uncertainty concerning things like recovery effort and reporting rates, but they can be used to estimate commercial selectivity. In the case of a single experiment, a straightforward plot of short-term recovery rate by length at release will show how selectivity changes with length. The absolute recovery rates will depend on usually unknown factors (tagging, fishing, and natural mortality rates; tag loss and reporting rates), but the relative recovery rates should depend mainly on selectivity (barring large variations in length with any of the unknown factors).

Myers and Hoenig (1997) showed how data from many experiments can be combined to obtain a single set of selectivity estimates. To summarize their derivation, let $\pi_{i,l}$ be the recovery rate of fish of length l in experiment i. This rate is treated as the product of a length-specific commercial selectivity s_l, which is the same for all experiments, and an experiment-specific recovery rate r_i that combines all the unknown factors mentioned above. Thus $\pi_{i,l}=r_i s_l$ and $\log\pi_{i,l}=\log r_i+\log s_l$. This has the form of a generalized linear model with a log link function and a binomial variance; therefore the point and variance estimates can be obtained in standard fashion.

Some rule has to be chosen for scaling the selectivities to make the model determinate. The most common rule is to require that the maximum selectivity be 1.0, but that can involve using a scaling factor that is poorly determined by the data if the maximum occurs in a length group with few releases and recoveries. To avoid this problem, the rule used in

Manuscript submitted 10 March 2005 to the Scientific Editor's Office.

Manuscript approved for publication 27 September 2005 by the Scientific Editor.

Fish. Bull. 104:465–467 (2006).

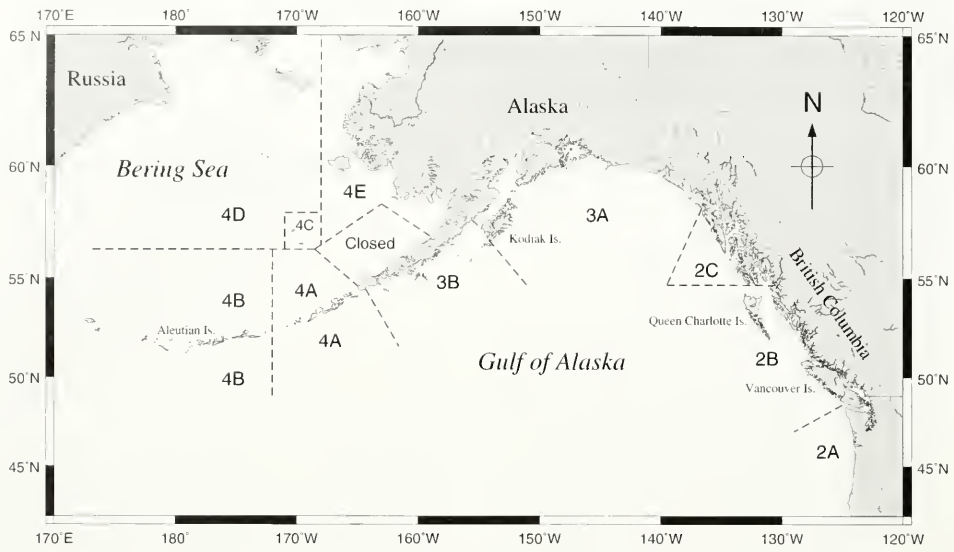

Figure 1

International Pacific Halibut Commission regulatory areas. The area marked "closed" is permanently closed to directed halibut fishing.

our study was to define selectivity to be 1.0 at 120 cm. Estimated selectivity could therefore exceed 1.0 at other lengths.

Results

Figure 2 shows the estimates of commercial length-specific selectivity in areas 2B, 2C, 3A, and 3B obtained by the method of Myers and Hoenig (1997) with the use of all available data in each area. There were insufficient data in area 4 to calculate useful estimates. The estimates in Figure 2 were calculated by using all recoveries from each release during the first two years at liberty, including recoveries from outside the release area and recoveries from unknown locations. Estimates computed by using only recoveries from the area of release were no different from those obtained by using all of the recoveries.

In all areas, commercial selectivity in the period of 1960–90 appears to increase with length up to a maximum and then decline. In area 2B, the peak occurs at about 110 cm and there is a substantial decline thereafter, to around half the peak value. In Alaska (areas 2C, 3A, 3B), selectivity peaks at a much larger size (about 150 cm). Thereafter the decline is about as steep as in area 2B, but not as large because so little of the length composition remains beyond 150 cm.

Recoveries from releases at spot fishing locations show a selectivity pattern similar to that for the entire dataset. The same is true of survey releases, except in area 2B where the selectivity pattern does not show a decline among larger fish. But this impression depends on a small number of recoveries, and therefore it may be false.

Discussion

In previous modeling of length-specific selectivity, the IPHC staff generally assumed some kind of asymptotic function, with full selection occurring at 110–130 cm. A function of this form is consistent with video observations of halibut behavior when they are hooked (Kaimmer, 1999), and it produces satisfactory fits to the observed length compositions of survey and commercial setline catches in the annual stock assessment. It is also consistent with the conventional view that hook selectivity varies little with size among fish large enough to take the bait (Lokkeborg and Bjordal, 1992). But the large body of mark-recapture data shows a different pattern: selectivity declining after the peak at 110 cm in area 2B, and not reaching a peak until 150 cm or so in Alaska. These patterns are, in fact, quite similar to those reported by Myhre (1969).

Commercial fishing selectivity reflects ground selection by the fleet, as well as size selection by the gear. It is therefore possible that the selectivity of commercial setline gear on a given ground has the expected asymptotic form, but ground selection has the effect of

targeting certain size groups and thereby producing a different selectivity schedule. In area 2B, for example, the best catch rates may be achieved by targeting smaller fish; whereas in Alaska it may be more profitable to target larger fish.

If the decline in selectivity in area 2B were the result of the commercial fishery targeting areas where the fish are smaller, one would expect to see the decline in data from survey releases (which are done over the whole area), but not in data from releases at spot fishing locations (most of which are customary commercial fishing locations). However, the mark-recapture data show the opposite pattern, if anything; therefore ground selection does not appear to be the explanation.

When length-specific selectivity is allowed to be dome-shaped in the stock assessment model (rather than forced to be asymptotic), the estimated commercial selectivities turn out to be quite similar in pattern to the mark-recapture estimates, including the differences among areas. But the selectivities estimated for the IPHC systematic setline survey are asymptotic or ramp-shaped, rather than dome-shaped. They indicate that ground selection by the commercial fishery really does have an effect on the form of commercial selectivity, contrary to what the mark-recapture data may indicate.

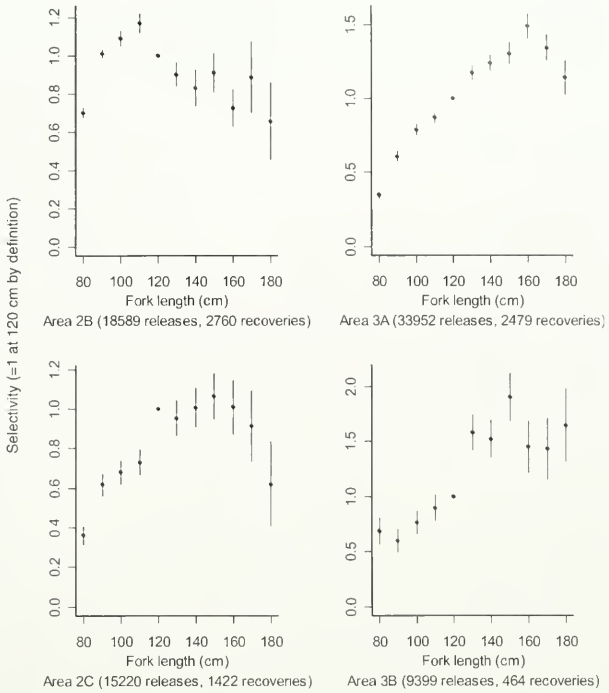

Figure 2

Estimates of length-specific commercial selectivity (±1 standard deviation) for Pacific halibut (*Hippoglossus stenolepis*) based on all releases 1960–90, by regulatory area. The scale was set by defining selectivity to be 1.0 at 120 cm, so that value has no standard deviation, and other values can and do exceed 1.0.

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Hatching date, nursery grounds, and early growth of juvenile walleye pollock (*Theragra chalcogramma*) off northern Japan*

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Walleye pollock (*Theragra chalcogramma*) is widely distributed in the North Pacific Ocean and plays an important role in coastal subarctic ecosystems. The Japanese Pacific population of this species is one of the most important demersal fishes for commercial fisheries in northern Japan. The population is distributed along the Pacific coast of Hokkaido and the Tohoku area (Fig. 1), which is the southern limit of distribution of the species in the western North Pacific. In Funka Bay, the main spawning ground for this population, pollock spawn from December to March (Kendall and Nakatani, 1992). Planktonic eggs and larvae are transported into the bay, where juveniles usually remain until late July when they reach 60–85 mm in total length (Hayashi et al., 1968; Nakatani and Maeda, 1987). These juvenile pollock then migrate from Funka Bay eastward to the Doto area off southeastern Hokkaido (Honda et al., 2004). Many studies on eggs, larvae, and juveniles of the species have been conducted in or near Funka Bay, but little information is available on the ecology of the early life stages in the Tohoku area. Hashimoto and Ishito (1991) suggested that eggs are transported from Funka Bay southward to the Tohoku area by the coastal branch of the Oyashio Current, but there has been no study to verify this hypothesis.

The aim of the present study was to examine, by using otolith daily growth ring analysis, regional differences in hatching date, body size, and early growth of juvenile pollock in Funka Bay and the Tohoku area and to elucidate the importance of Tohoku area as a nursery ground for the Japanese Pacific population of pollock.

Materials and methods

The present study was carried out from Funka Bay to the Tohoku area. We divided the study area into four regions, Funka Bay, east of Tsugaru Strait, northern Tohoku, and southern Tohoku (Fig. 1). East of Tsugaru Strait region is located between Funka Bay and the Tohoku area. Sampling was done at a total of 54 stations mostly in late May during three years, from 1999 to 2001: 10 for 1999, 23 for 2000, and 21 for 2001 (Table 1). In Funka Bay, sampling stations were set up only at the bay mouth area because there was a lot of fishing gear inside the bay. Pollock juveniles were collected with a midwater trawl (NST-92-K1, Nichimo Co., Ltd., Shinagawa, Tokyo) onboard the RV *Wakataka Maru* of the Tohoku National Fisheries Research Institute (TNFRI).

The midwater trawl, which had a round mouth opening with a diameter of about 20 m, was towed only during the day. The overall length of the net was 98.3 m and it had a variable-size mesh of 14 m (stretched) in the forward section to 3 mm (square mesh) at the codend. All tows were made at an average ship speed of 4 knots. The horizontal tows were carried out in 1999, whereas the double oblique tows were made from the surface to near the bottom (10–20 m above the bottom) in 2000–2001. The sampling biases of the net were not investigated, but biases may have been neglible for two reasons. First, our net had a larger mouth opening than that of the Methot trawl (5 m^2) used for collecting late larval and early juvenile stages of walleye pollock (Brodeur et al., 1995). Second, we could sample juveniles that hatched from mid-December to mid-April in our survey and the juveniles were thought to be from eggs that spawned throughout the whole spawning season (December to March) in Funka Bay.

Pollock juveniles were sorted from the codend samples and preserved in 95% ethanol diluted with seawater for otolith daily-growth analysis. Total length (TL) of some pollock was measured to the nearest 0.1 mm on board the vessel, whereas the same length of preserved fish was similarly measured in the laboratory. The following formula was used to change TL of preserved fish to TL of fresh fish:

* Contribution number B63 from Tohoku National Fisheries Research Institute, Fisheries Research Agency, Shinhama, Shiogama, Miyagi, Japan.

Manuscript submitted 29 July 2004
to the Scientific Editor's Office.
Manuscript approved for publication
27 September 2005 by the Scientific Editor.
Fish. Bull. 104:468–475 (2006).

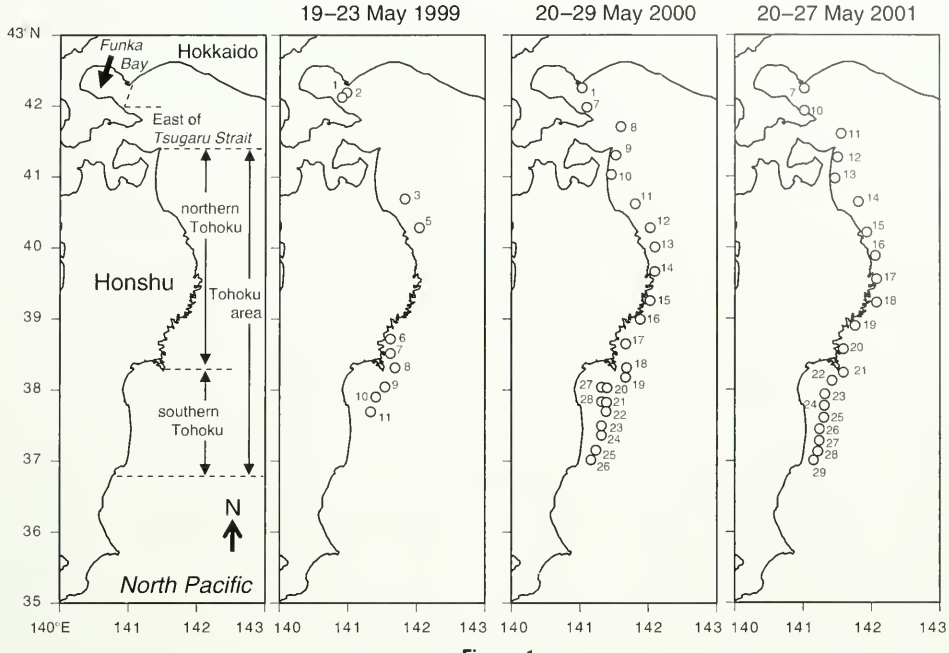

Figure 1

Sampling stations (open circles) for walleye pollock (*Theragra chalcogramma*) caught with a midwater trawl net in four regions off the Pacific coast of northern Japan in May 1999–2001. Arabic numerals indicate station numbers (see Table 1).

TL of fresh fish = 1.0126(*TL of preserved fish*) + 1.7934 [n=97, r^2=0.974].

To study the daily otolith increment of our sample, we employed the methods established by Nishimura and Yamada (1984), Bailey and Stehr (1988), Yoklavich and Bailey (1990) and Bailey et al. (1996). Sagittal otoliths, hereafter called "otoliths," from the juveniles were embedded in epoxy resin on glass slides and ground with carbon paper (no. 800–1200) perpendicularly to the otolith flat plane along the long axis (frontal section). Polished otoliths were selected if they included the otolith nucleus on the ground surface and were thin enough to transmit light under a light microscope. Then 1171 specimens were polished with lapping film, cleaned, and observed. Early narrow increments were counted under 600× or 1000× magnification. As the increments increased in width, the magnification was changed to 400×. Hatching date was estimated by subtracting the number of increments from the sampling date.

Daily growth-ring diameter is the index of body length at an age because a significant linear relationship exists between log-transformed body length and otolith length data for pollock juveniles (Nishimura and Yamada, 1988). In the present study, we measured the short otolith radius (SOR) along the long axis obtained from a frontal section and used the SOR from the nucleus to the 30th ring (SOR 30) as the index of early growth. SOR 30 was measured for the specimens collected in 2000, by using the otolith daily growth ring analyzing system (Ratoc System Engineering Co., Ltd., Shinjuku, Tokyo). The Mann-Whitney U-test was used to identify differences in SOR 30 groups. We were not able to use analysis of covariance (ANCOVA) because an interaction was found by analysis of variance (ANOVA) in size-at-age relationships among regions in 2000 (P<0.0001) and 2001 (P=0.035). Comparisons of specific growth rate (SGR) for the juveniles were made between our regions by the Mann-Whitney U-test or ANOVA. Comparisons of means were made using Scheffe's test. SGR values of individual fish were calculated by using the following formula (Ricker, 1979):

$$SGR = \frac{(\ln L_2 - \ln L_1) \times 100}{t_2 - t_1},$$

Table 1

Summary of midwater trawl surveys in May of 1999–2001. SST=sea surface temperature, OB= oblique tow, HZ=horizontal tow.

Station no.	Sampling date	Depth (m)	SST (°C)	Towing time (min)	Method	Number of fish	CPUE (fish/h)
1	19 May 1999	69	7.2	63	HZ	6	5.7
2	19 May 1999	69	7.2	70	HZ	129	110.6
3	21 May 1999	99	10.6	72	HZ	4	3.3
5	21 May 1999	108	10.7	84	HZ	19	13.6
6	23 May 1999	97	11.2	88	HZ	0	0
7	23 May 1999	124	11.8	74	HZ	0	0
8	23 May 1999	136	11.6	93	HZ	0	0
9	22 May 1999	106	14.7	98	HZ	0	0
10	22 May 1999	102	16.4	84	HZ	0	0
11	22 May 1999	100	17.1	49	HZ	0	0
1	20 May 2000	84	8.4	45	OB	730	973.3
7	21 May 2000	101	8.3	57	OB	173	182.1
8	21 May 2000	111	9.6	48	OB	399	498.8
9	21 May 2000	90	10.1	42	OB	0	0
10	22 May 2000	123	10.8	50	OB	6	7.2
11	22 May 2000	111	9.2	51	OB	17	20.0
12	22 May 2000	107	10.9	54	OB	69	76.7
13	25 May 2000	121	11.3	62	OB	90	87.1
14	25 May 2000	151	10.9	48	OB	14	17.5
15	25 May 2000	138	10.9	43	OB	163	227.4
16	26 May 2000	122	11.0	49	OB	57	69.8
17	26 May 2000	133	13.1	48	OB	81	101.3
18	26 May 2000	143	13.7	51	OB	24	28.2
19	26 May 2000	121	14.3	51	OB	22	25.9
20	27 May 2000	104	12.5	48	OB	62	77.5
21	27 May 2000	122	13.7	48	OB	37	46.3
22	27 May 2000	130	12.8	57	OB	29	30.5
23	27 May 2000	97	12.5	44	OB	37	50.5
24	27 May 2000	105	12.9	51	OB	11	12.9
25	28 May 2000	77	9.7	60	OB	11	11.0
26	28 May 2000	102	9.9	50	OB	35	42.0
27	29 May 2000	69	13.3	47	OB	144	183.8
28	29 May 2000	82	12.6	45	OB	15	20.0
7	20 May 2001	71	10.2	55	OB	51	55.6
10	20 May 2001	103	7.6	39	OB	2371	3647.7
11	22 May 2001	117	10.4	48	OB	1	1.3
12	22 May 2001	90	11.0	40	OB	0	0
13	22 May 2001	176	10.5	48	OB	10	12.5
14	23 May 2001	109	10.3	51	OB	11	12.9
15	23 May 2001	104	10.6	52	OB	106	122.3
16	23 May 2001	120	13.1	45	OB	117	156.0
17	24 May 2001	141	11.7	60	OB	19	19.0
18	24 May 2001	147	11.5	44	OB	6	8.2
19	24 May 2001	108	10.7	23	OB	2	5.2
20	25 May 2001	130	10.5	31	OB	0	0
21	25 May 2001	115	11.2	23	OB	2	5.2
22	25 May 2001	112	11.6	45	OB	1	1.3
23	25 May 2001	104	12.0	22	OB	0	0
24	26 May 2001	120	13.4	42	OB	0	0
25	26 May 2001	125	12.0	57	OB	0	0
26	26 May 2001	97	12.1	35	OB	0	0
27	27 May 2001	106	15.7	35	OB	0	0
28	27 May 2001	100	19.1	52	OB	0	0
29	27 May 2001	103	19.6	21	OB	0	0

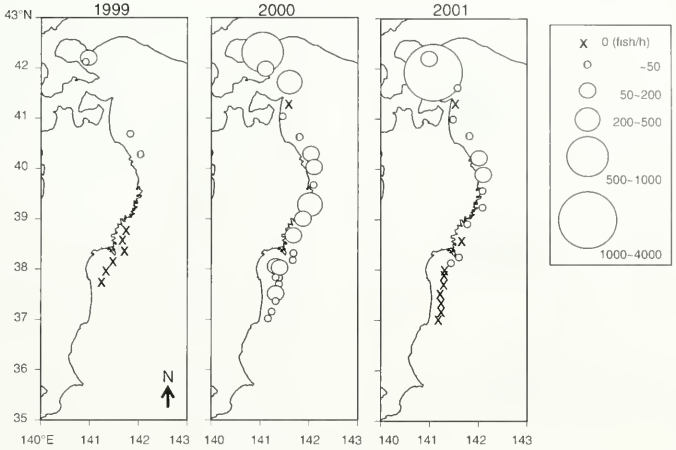

Figure 2

Distribution of catch per unit of effort (CPUE) (fish/hour) for walleye pollock (*Theragra chalcogramma*) caught with a midwater trawl net in May 1999–2001 off the Pacific coast of northern Japan.

where L_2 and L_1 = body length at time t_2 and t_1, respectively.

In this study, we defined $L_1 = 4.6$ mm at hatching ($t_1 = 0$) according to Nishimura and Yamada (1988) and L_2 = TL of fish at the number of otolith increments (t_2). All tests were evaluated for significance at the $P = 0.05$ level.

Results and discussion

Distribution of juveniles

In 1999, juvenile pollock were collected only from Funka Bay to northern Tohoku, but no fish were sampled in southern Tohoku (Fig. 2). In 2000, juvenile pollock were caught in abundance at almost all sampling stations: highest catch per unit of effort (CPUE) was recorded at a station in Funka Bay (973 fish/h) and many juveniles were found in northern and southern Tohoku (max: 227 and 184 fish/h, respectively). In 2001, the juvenile distribution was similar to that in the previous year, but few juveniles were caught in southern Tohoku. These results show interannual variability in the distribution of juvenile walleye pollock between 1999 and 2001.

Inada and Murakami (1993) suggested that the pollock catch and distribution in the Tohoku area are strongly affected by the coastal branch of the Oyashio Current but little information is available on the relationship between oceanographic conditions and juvenile distribution and abundance in this area. The southern limit of the coastal branch characterized by the position of 5°C at 100 m depth has been regarded as an index to show the strength of the current (Ogawa, 1989). Thus we examined annual changes in the position of southern limit of the coastal branch based on water temperature data (TNFRI[1]). In April, the coastal branch of the Oyashio Current mostly stagnated in northern Tohoku in 1999 and 2001 but there were some annual variations, but it went far south to southern Tohoku in 2000 (Fig. 3A). It is likely that the juvenile distribution in May of the three years from 1999 to 2001 is associated with the southern limit position of the coastal branch of the Oyashio Current in April. Kitagawa et al.[2] reported the recruitment index of age-0 pollock based on bottom trawl surveys in the Tohoku area. We compared the recruitment index (X, $\times 10^3$ fish) given by Kitagawa et al.[2] with the latitude of the southern limit of the coastal branch of the Oyashio Current (Y) and, as a result, a significant relationship was observed in the 1995–2001 data ($Y = 46.653X^{-0.019}$, $r^2 = 0.960$, Fig. 3B). This result may indicate that abundant recruitment is brought by

[1] TNFRI (Tohoku National Fisheries Research Institute). 1997–2002. Tohoku Block Suisan Kaiyo Renraku Kaihou, vols. 26–32. TNFRI, Fisheries Oceanography Division, 3-27-5 Shinhama-cho, Shiogama, Miyagi 985-0001, Japan. [In Japanese.]

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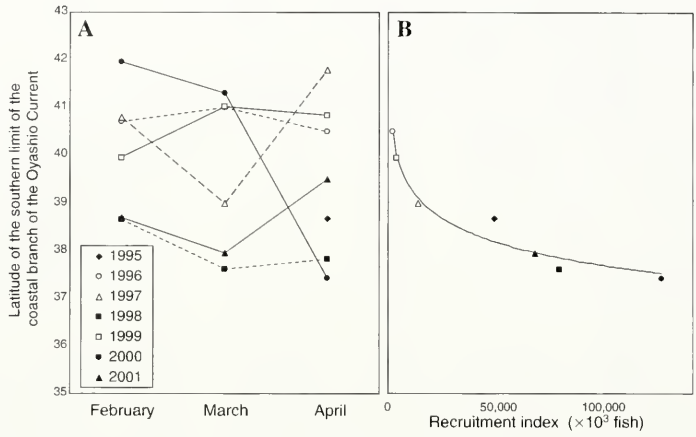

Figure 3

Monthly change in the latitude of the southern limit of the coastal branch of the Oyashio Current (**A**), and the relationship between recruitment index of age-0 walleye pollock (*Theragra chalcogramma*) in the Tohoku area and the latitude of the southern limit of the coastal branch of the Oyashio Current (**B**). This figure is drawn according to the water temperature data from the Fisheries Oceanography Division of the Tohoku National Fisheries Research Institute (TNFRI) (see text). The data on the recruitment index are from Kitagawa et al.[2] (see general text).

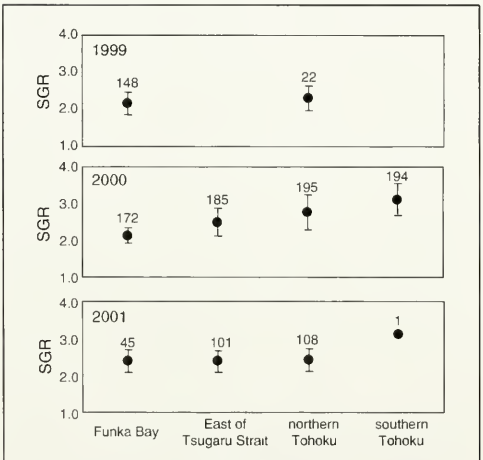

Figure 4

Specific growth rate (SGR) for walleye pollock (*Theragra chalcogramma*) from four regions off the Pacific coast of northern Japan in 1999–2001. Vertical bars indicate standard deviation and arabic numerals indicate number of samples.

a strong coastal branch of the Oyashio Current in the Tohoku area.

Early growth of walleye pollock

There was no difference in SGR between Funka Bay and northern Tohoku in 1999 (U-test, $P=0.111$, Fig. 4). Also, no regional differences were found among all regions in 2001 (ANOVA, $P=0.526$). For 2000, however, there were significant differences in SGR among all four regions (ANOVA, $P<0.0001$) and even between all pairs (Scheffe's test, $P<0.0001$).

In 2000, the SOR 30 values ranged from 30–58 μm for the juveniles collected in Funka Bay and east of Tsugaru Strait (Fig. 5). However, two different SOR 30 groups were found for the samples from northern and southern Tohoku (U-test, $P<0.0001$): one with SOR 30 values ranging from 30–60 μm and the other with values greater than 68 μm. Fish of the former group (low-growth group) had the same SOR 30 range as those from Funka Bay and east of Tsugaru Strait. The latter group (high-growth group) was observed only in the Tohoku area. Positive linear regressions were found in size-at-age relationships for low- and high-growth groups ($P<0.0001$, Fig. 6) and the difference of the SGR was significant between these two groups (U-test, $P<0.0001$).

These results indicate that the surveys of juvenile walleye pollock in May 2000 caught two growth groups:

the low-growth group that probably spawned in Funka Bay mixed with the high-growth group that was probably produced locally in the Tohoku area. This mixing of the two groups could have occurred primarily because of either advection or migration. Assuming that this interpretation is correct, it would be important for local fisheries managers to take account of these variations especially if the years of extra production from the Tohoku area expand the exploitable stock.

Length-frequency distribution and hatching date

The length-frequency distribution and hatching date composition for juvenile pollock among regions were similar in 1999 and 2001 but were different in 2000 (Figs. 7 and 8). In 2000, large fish over 40 mm TL, designated as forming part of the low-growth group, constituted the majority of the samples from Funka Bay, and much smaller fish of the same group (<40 mm TL) were widely distributed in waters from east of Tsugaru Strait to southern Tohoku. All juveniles from Funka Bay were categorized as low-growth group fish that hatched between late December and late February, and juveniles of the low-growth group that hatched after March 1 were caught widely from east of Tsugaru Strait to southern Tohoku in 2000. These results appear to indicate that late hatching fish originating from Funka Bay were transported to the Tohoku area by the strong coastal branch of the Oyashio Current after March 2000.

Nakatani and Sugimoto[3] showed that only fish hatching in January and February survived in Funka Bay in summer, whereas pollock usually spawn between December and March. Nakatani (1998) thus assumed that late hatching fish (after early March) would not be able to consume enough food during their settlement stage because the abundance of copepodids of *Pseudocalanus* spp., the main food for juveniles below 30 mm TL, decreases in late May and because late hatching fish cannot eat *Neocalanus plumchrus* due to its large size. Therefore, he suggested that there are two critical periods for walleye pollock during their early larval and settlement stages in Funka Bay. Considering these results, we suggest that when late hatching fish were transported to the Tohoku area, their survival rates were higher than those of juveniles that remained in Funka Bay.

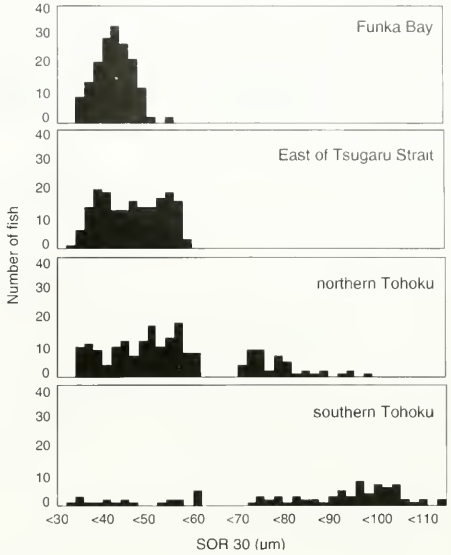

Figure 5

Frequency distribution of the short otolith radius from the nucleus to the 30th ring (SOR 30) for walleye pollock (*Theragra chalcogramma*) collected in four regions off the Pacific coast of northern Japan in 2000.

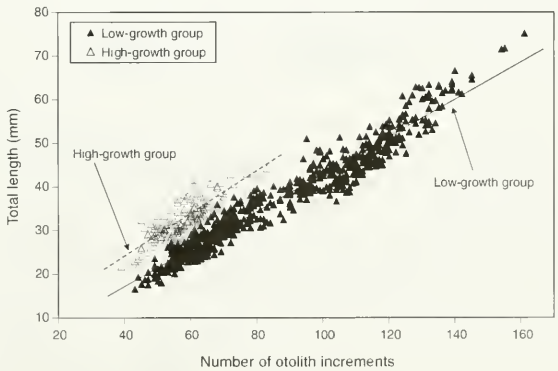

Figure 6

Size-at-age relationship for two growth groups of walleye pollock (*Theragra chalcogramma*) collected in 2000. Low- and high-growth groups were divided according to the SOR 30 distribution (see text and Fig. 5). The regression lines for each growth group are as follows: low-growth group: $TL=0.017+0.429\times age$ [$r^2=0.941$, $n=594$, $P<0.0001$]; high-growth group: $TL=4.694+0.486\times age$ [$r^2=0.715$, $n=152$, $P<0.0001$].

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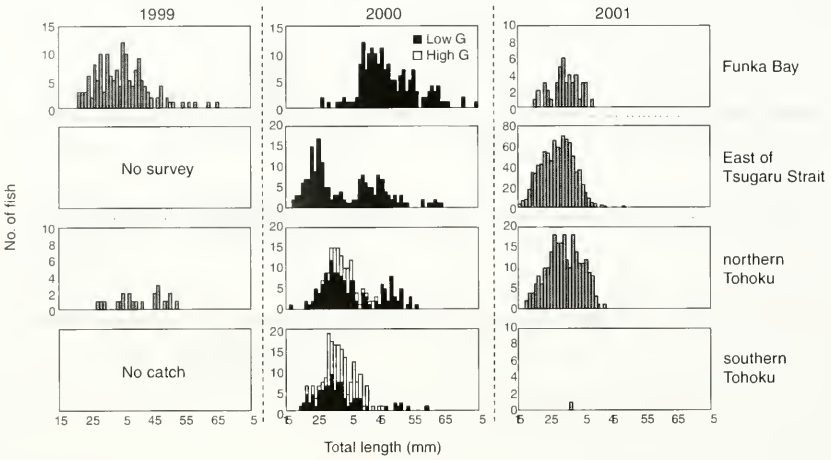

Figure 7

Total length-frequency distribution for walleye pollock (*Theragra chalcogramma*) from four regions off the Pacific coast of northern Japan in 1999–2001. Low G=low-growth group (solid bars); high G=high-growth group (open bars).

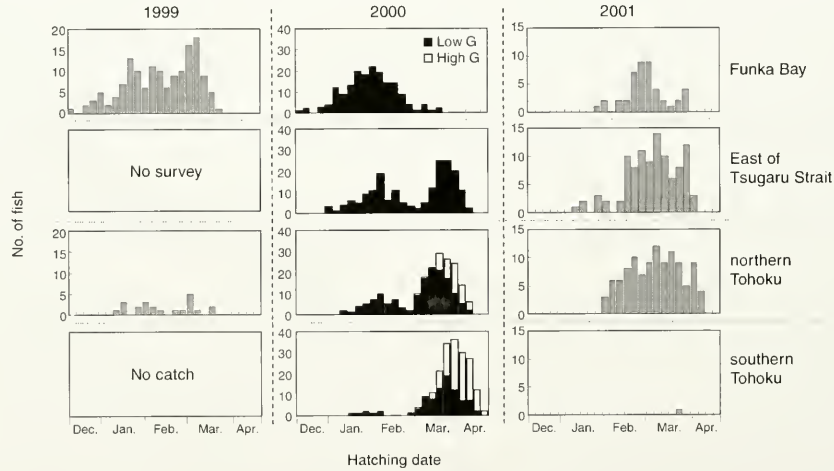

Figure 8

Hatching date composition for walleye pollock (*Theragra chalcogramma*) from four regions off the Pacific coast of northern Japan in 1999–2001. Low G=low-growth group (solid bars), high G=high-growth group (open bars).

We suggest that, in addition to the recruitment process in Funka Bay, an important recruitment process occasionally exists in the Tohoku area, and when the year-class strength of the Japanese Pacific population of pollock is strong, as in 2000 (Yabuki[4]), the Tohoku area becomes important as a nursery ground for the late hatching fish originating from Funka Bay.

Acknowledgments

We thank the crew of the RV *Wakataka Maru* who endured long working hours to obtain the samples used in this study. We also thank Yasunori Sakurai of the Graduate School of Fisheries Sciences, Hokkaido University, Yoshioki Oozeki of the National Research Institute of Fisheries Science, Fisheries Research Agency, and Kazuya Nagasawa of the Tohoku National Fisheries Research Institute, Fisheries Research Agency, for their advice and helpful discussions. We thank the anonymous reviewers who improved the draft of this article. This research was funded by the VENFISH Program of the Ministry of Agriculture, Forestry and Fisheries.

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Development of larval and early juvenile penpoint gunnel (*Apodichthys flavidus*) (family: Pholidae)

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The penpoint gunnel (*Apodichthys flavidus*) is a member of the perciform family Pholidae. Pholids, commonly referred to as gunnels, are eel-like fishes that inhabit the rocky intertidal and subtidal regions of the northern oceans and are often associated with macroalgae, such as *Fucus* spp. or kelp (Watson, 1996). Gunnels are ecologically important forage fishes that form part of the diet of birds and commercially important groundfish species (Hobson and Sealy, 1985; NMFS[1]; Golet et al., 2000). The diet of *A. flavidus* and other pholids comprises primarily harpactacoid copepods, gammarid amphipods, isopods, and other crustaceans (Cross, 1981). *Apodichthys flavidus* ranges along the west coast of North America from southern California to the Gulf of Alaska (Mecklenburg et al., 2002). Adult *A. flavidus* are distinguished from other pholids by their total vertebral counts, the presence of a thick and grooved first anal spine, a preanal length that is approximately 60% standard length (SL), and a dark green to light olive coloration (Yatsu, 1981). It is one of the largest pholids (up to 46 cm) and is important in the live fish trade for both home and public aquaria (Froese and Pauly[2]).

In late winter to early spring months (January–April), adult *A. flavidus* spawn in nearshore waters. A single female lays clusters of demersal, adhesive eggs onto substrate that a male will guard until hatching (Clemens and Wilby, 1961; Wilkie, 1966; Marliave, 1975). The eggs are 3 mm in diameter and the incubation period is approximately 2.5 months (Wilkie, 1966; Marliave, 1975). Larvae are about 12–13 mm total length (TL) at the time of hatching, well developed, and have pigmented eyes, an elongated body, and very little to no yolk sac (Wilkie, 1966; Marliave, 1975). After about 50 days, the larvae settle as juveniles and are approximately 25 mm SL (Marliave, 1975). Although *A. flavidus* reproduction has been well-studied, there has not been a complete description of larval development. Wang[3] provided a summary of life history information and pencil illustrations of early flexion, postflexion, and juvenile stages. Matarese et al. (1989) published an illustration of a 15.0-mm flexion larva and some characters distinguishing *A. flavidus* from *Pholis* spp.

In the present study we describe development of *A. flavidus* from recently hatched larvae to newly settled juveniles, including some general aspects of osteological development. Larval *A. flavidus* are compared with larvae of other pholid species included in the genus *Apodichthys* by Yatsu (1981, 1985): *Xererpes fucorum* and *Ulvicola sanctaerosae*. This classification was not followed by Matarese et al. (1989) or Watson (1996) and is not followed in the present study. This work will aid in the accurate identification of *A. flavidus* larvae in samples taken during nearshore ichthyoplankton surveys and in ecological studies and will contribute to a better understanding of pholid systematics.

Materials and methods

We examined 58 larval and juvenile *A. flavidus* (11.9–42.3 mm) collected in dip-net surveys by scientists of the Alaska Fisheries Science Center (AFSC; Busby et al., 2000) and the University of Washington (UW) from four sites: Clam Bay (47°34.5′N, 122°32.5′W), Sequim Bay (48°2.3′N, 123°2.0′W), Iceberg Point (48°42.4′N 122°53.3′W), and Friday Harbor (48°54.5′N, 1230.7°W), all located in

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Manuscript submitted 22 June 2005 to the Scientific Editor's Office.
Manuscript approved 24 October 2005 by the Scientific Editor.
Fish. Bull. 104:476–481 (2006).

Puget Sound, WA, and from adjacent waters. Specimens were initially preserved in 3.5% buffered formalin solution and later transferred to 70% ethanol (Busby et al., 2000). A dissecting stereomicroscope was used to examine pigmentation, general body size and structure, and to obtain meristic counts. Morphological measurements were made on 55 suitable specimens by using a digital image analysis system consisting of a video camera attached to a dissecting stereomicroscope and a computer with image analysis software. All measurements were taken from the left side of the specimen. Standard length was used throughout the study unless otherwise indicated. During flexion stage, notochord length (NL) was measured and recorded as SL. Measurements included standard length, head length, eye diameter, body depth, snout to anus length, and pectoral-fin length, as described by Moser (1996).

To describe osteological development of *A. flavidus*, with emphasis on the development of the caudal skeleton, 12 specimens were cleared and stained by using the technique described by Potthoff (1984). The terms "unossified precursor" or "element" are used to describe unossified elements that took up alcian blue stain but not alizarin red-s stain. From the cleared and stained specimens, stages of larval development were identified from landmarks of caudal-fin development. Caudal skeletons of six specimens representing distinct stages were used to create illustrations. Developmental stage terms follow Kendall et al. (1984) and Neira et al. (1998). The flexion stage was divided into three additional stages: early-, mid- and late-flexion. Early-flexion begins at hatching, mid-flexion begins with the formation of the forth hypural and epurals, and late flexion begins with the development of the fifth hypural and ends with complete notochord flexion. Nomenclature of caudal skeleton elements follows Fujita (1989).

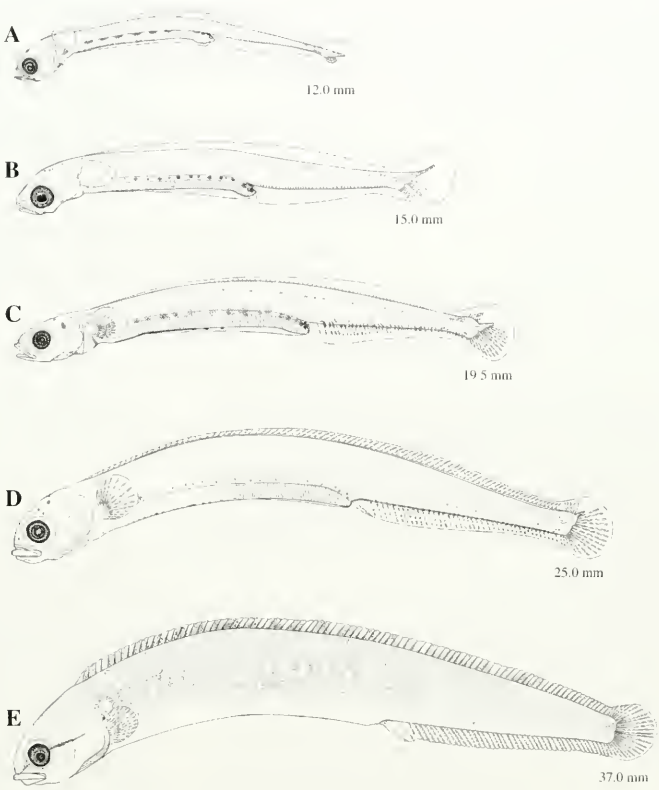

Figure 1

Developmental series of penpoint gunnel (*Apodichthys flavidus*).(**A**) Early-flexion larva, Clam Bay, 6 April 1989 (UW 104928); (**B**) mid-flexion larva (from Matarese et al., 1989); (**C**) late-flexion larva, Friday Harbor, 20 April 1994 (UW 104930); (**D**) postflexion larva, Clam Bay, 20 April 1989 (UW 104932); (**E**) juvenile, Sequim Bay, 25 April 1989 (UW 104934). Illustrations by Beverly Vinter.

Results

Morphology

Apodichthys flavidus larvae are approximately 12.0–13.0 mm at hatching and in early flexion stage and have little or no yolk sac present (Fig. 1A). The early-flexion stage occurs between hatching and 14.0 mm. Mid-flexion begins at approximately 14.0 mm (Fig. 1B), late-flexion at 17.0 mm (Fig. 1C), and postflexion at 20.0 mm (Fig. 1D). Transformation to the juvenile stage occurs between 25.0 mm and 30.0 mm. Juveniles examined ranged from 30.1 to 42.3 mm and looked like small

Table 1

Body proportions of larval and early juvenile penpoint gunnel (*Apodichthys flavidus*). Values given for each body proportion are expressed as percentages of standard length (SL) or head length (HL): mean ± standard deviation, and range.

Sample size, standard length, and body proportion	Flexion	Postflexion	Juvenile
Sample size	33	18	4
Standard length (SL)	14.9 ±2.1 (11.9–19.2)	21.9 ±1.3 (20.0–24.0)	34.2 ±5.6 (30.1–42.3)
Snout to anus length/SL	62.9 ±1.8 (58.0–66.1)	63.3 ±1.2 (61.8–66.1)	63.5 ±1.8 (62.5–65.2)
Body depth/SL	8.3 ±0.9 (6.4–9.9)	9.3 ±0.7 (8.2–10.4)	11.6 ±1.1 (11.2–12.9)
Head length/SL	13.2 ±0.7 (12.1–14.8)	14.1 ±0.7 (12.9–15.5)	16.4 ±1.1 (15.3–17.3)
Eye diameter/HL	33.6 ±4.7 (22.3–44.1)	27.4 ±3.1 (23.5–35.4)	20.0 ±3.9 (15.8–24.8)
Pectoral fin length/SL	7.6 ±1.2 (5.4–10.2)	7.9 ±1.0 (6.2–10.1)	6.2 ±1.4 (4.9–7.1)

adults (Fig. 1E). Larvae are slender bodied throughout development and body depth increases from 8% SL during flexion to 12% SL in juveniles (Tables 1 and 2). Head, snout-to-anus, and pectoral-fin lengths are consistent throughout development at approximately 14%, 63%, and 7% SL, respectively. Eye diameter decreases from 34% head length (HL) in flexion larvae to 20% HL in juveniles.

Pigmentation

Early-flexion larvae have a few faint melanophores located dorsally on the head and nape and a single melanophore on the isthmus (Fig. 1A). Along the dorsal surface of the gut, a row of large melanophores is present—irregularly spaced anteriorly and posteriorly, regularly spaced medially. Another row of smaller, evenly spaced melanophores is present along the anterior ½ to ¾ length on the ventral surface of the gut. A row of postanal ventral melanophores (PVMs) extends from the anus to the caudal peduncle. Generally there is one PVM per myomere but in many individuals one or more are missing from the row. In addition, there are small patches of melanophores along the dorsal and ventral margins of the caudal peduncle. In mid-flexion larvae, patches of melanophores on the head, nape, isthmus, and caudal peduncle are more defined, and a row of internal melanophores is present above the notochord (Fig. 1B). These melanophores develop simultaneously. In addition, the number of melanophores along the dorsal surface of the gut nearly doubles. The PVMs in late-flexion larvae are larger and more slashlike (Fig. 1C). During postflexion, pigmentation previously noted now appears very faint (Fig. 1D). Juvenile pigmentation resembles that of adults (Fig. 1E). Most notably, a horizontal streak of melanophores extends from the snout to the anterior margins of the eye and continues from the posterior margin of the eye to the mid-operculum. The body in live specimens is a uniform bright green to olive and has white spots located above the gut and anterior portion of the anal fin. The gut is generally unpigmented, with the exception of a few very small irregularly spaced melanophores on the lateral surface.

Osteology

Head region In early-flexion larvae the maxilla, mandible, two mandibular teeth, branchiostegal rays, and cleithrum are ossified. The premaxilla ossifies during mid-flexion. The remaining bones in the head region are not ossified until the juvenile stage.

Fins Unossified precursors of five principal caudal-fin rays are present at hatching and throughout early flexion. During mid-flexion, 12 unossified precursors of pectoral-fin rays and 13 unossified caudal-fin elements are present, both first appearing at 15.0 mm. Also at this size, a few faint unossified anal-fin elements are present in the anterior portion of the anal finfold, which are not visible in unstained specimens. Beginning at 17.0 mm, unossified precursors of dorsal-fin spines are first present in the area of the dorsal finfold above vertebrae 45–50 and then develop anteriorly and posteriorly from this position. Unossified anal-fin elements are also added from anterior to posterior. In addition, the scapula, coracoid, and radials of the pectoral fin are ossified and the adult complement caudal-fin elements is present, but still unossified (13 principal rays and 11 procurrent rays). By the end of late flexion (about 20.0 mm), elements of the dorsal, anal, and pectoral fins finally become ossified (Table 2). The single spine is the first element in the anal fin to become ossified. Pterygiophores of all fins are ossified in juveniles and the pectoral- and caudal-fin rays become ossified and branched. The number of fin elements present at any particular stage and length is somewhat variable as we noted slight differences in the numbers present between our stained and illustrated specimens.

Vertebral column At hatching, all neural and haemal spines are present and ossified (Table 2). In addition, vertebral centra begin to differentiate from anterior to

posterior during the early- and mid-flexion stages. At 17.0 mm, the vertebral centra are completely differentiated but remain unossified. In juveniles, the vertebral centra are completely ossified.

Caudal skeleton In early flexion larvae, the notochord begins to bend upward and the haemal spine of the second preural centrum, the fused parhypural plus first and second hypurals, and the third hypural are present (Fig. 2A). Caudal skeleton elements begin to ossify at this stage, beginning at the base of each. Ventral elements that develop at mid-flexion are the haemal spine of the third preural centrum and the fourth hypural (Fig. 2B). Dorsally, epurals 1–3 and neural spines of the second and third preural centra form during this stage. Elements present in early-flexion are now fully ossified. At the beginning of late-flexion (about 17.0 mm), a fifth hypural and a fourth epural are present but not ossified (Fig. 2C). In the 19.2-mm late-flexion specimen examined, the third and fourth epurals were fused and the first epural was fused to the neural spine of the second preural centrum (Fig. 2D). In postflexion larvae, the distal margins of hypurals 3–5 are oriented vertically and the first epural separates from the neural spine of the second preural centra (Fig. 2E). All other elements in the caudal skeleton have grown and are fully ossified. In juveniles, the caudal fin has the adult form and the final element, the uroneural, is present just ventral to the second and fused third and fourth epurals (Fig. 2F). A ventral caudal radial, present from mid-flexion to postflexion (Figs. 2, C–E), is absent in juveniles.

Discussion

Our description of *A. flavidus* development can be used to distinguish larvae of this species from co-occurring species of *Pholis* spp., *Apodichthys*, *Ulvicola*, and *Xererpes* along the West Coast of the United States. As with *Ulvicola sanctaerosae*, *A. flavidus* does not have a preflexion stage and larvae hatch at an advanced developmental state (Watson, 1996). Larval *Pholis* spp. differ from larval *A. flavidus* by the presence of pelvic fins in the former and by differences in pigmentation. The melanophores along the dorsal surface of the gut in *Pholis* spp. are more numerous (about 25 vs. about 18 in postflexion larvae) and closer in spacing anteriorly (Matarese et al., 1989), and *Pholis* spp. do not develop an internal row of melanophores along the dorsal margin of the notochord. *Apodichthys flavidus* develops a series of internal melanophores along the entire length of the notochord by the mid-flexion stage. Larvae of *U. sanctaerosae* can be distinguished from *A. flavidus* by pigmentation and by the number and persistence of pectoral-fin rays in postflexion larvae and juveniles. Larval *U. sanctaerosae* have fainter melanophores that are more irregularly spaced along the dorsal

Table 2

Meristics of cleared and stained larval and early juvenile penpoint gunnel (*Apodichthys flavidus*). Counts are of ossified elements only. Specimens above dashed line (- - - -) were undergoing notochord flexion.

Standard length (mm)	Dorsal-fin spines	Anal-fin elements	Pectoral -fin rays	Branchiostegal rays	Neural spines			Haemal spines	Centra			Caudal-fin rays
					abdominal	caudal	total		abdominal	caudal	total	
12.2				5	50	43	93	44				
12.8				5	50	42	92	43				
13.4				5	51	45	96	44				
14.6				5	52	43	95	42				
15.0				5	51	43	94	44				
17.0				5	52	42	94	45				
19.2	XC	1	15	5	50	41	91	44				
21.2	XCI	1	15	5	50	43	93	45				
23.5	XCI	1	15	5	51	44	95	45				
30.1	XCII	1, 39	14	5	51	42	93	46	51	45	96	24
33.2	XCI	1, 41	15	5	50	43	93	43	50	45	95	24
42.3	XCI	1, 40	15	5	50	42	92	42	50	44	94	24

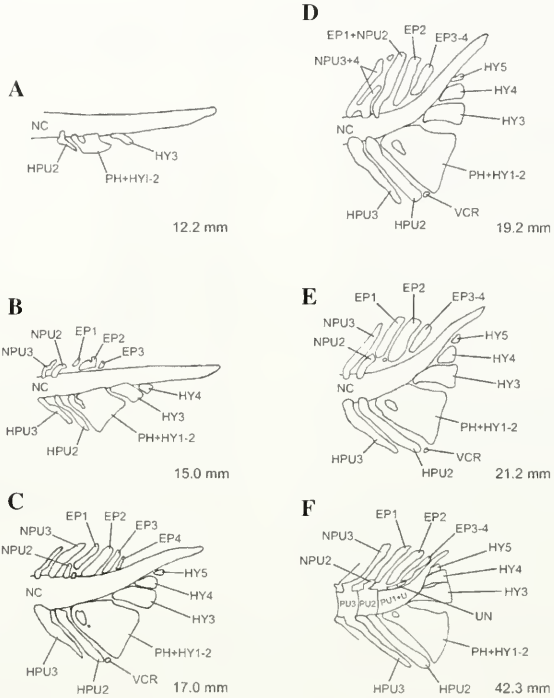

Figure 2

Caudal skeleton development of penpoint gunnel (*Apodichthys flavidus*). (**A**) Early-flexion larva, Clam Bay, 27 February 1995 (UW 104943); (**B**) mid-flexion larva (note irregularly shaped EP2), Clam Bay, 10 May 1989 (UW 104937); (**C**) late-flexion larva, Clam Bay, 19 April 1988 (UW 104939); (**D**) late-flexion larva, Clam Bay, 15 May 1989 (UW 104940); (**E**) postflexion larva, Friday Harbor, 8 April 1993 (UW 104943); (**F**) juvenile, Iceberg Point, 18 July 1963 (UW 018016). Caudal-fin element abbreviations: EP=epural; HPU=haemal spine, preural; HY=hypural; NC=notochord; NPU=neural spine, preural; PH=parhypural; PU=preural centra; U=urostyle; UN=uroneural; VCR=ventral caudal radial. Illustrations by Lisa De Forest.

surface of the gut than in *A. flavidus*, and in early- and mid-flexion larvae, these melanophores are restricted to the posterior ¼ to ½ of the gut. Another distinguishing characteristic is that *U. sanctaerosae* does not fully develop pectoral-fin rays and the pectoral fin does not persist after the juvenile stage. A pectoral finfold is present during the larval stage of this species; however, only the uppermost pectoral-fin rays (6 or 7 vs. 14 or 15 for *A. flavidus*) partially develop but do not persist, and the pectoral finfold decreases in size during the latter part of development. Larvae of *Xererpes fucorum* can be distinguished from *A. flavidus* by the presence of a preflexion stage and by having fewer total (84–93 vs. 96–101) and postanal (35–40 vs. 47–52) myomeres. In addition, during the later stages of development, *X. fucorum* has fewer pectoral-fin rays than *A. flavidus* (12 vs. 14–15).

Yatsu's (1985) revision of the family Pholidae placed *U. sanctaerosae* and *X. fucorum* in the genus *Apodichthys*, but this classification was not followed by Matarese et al. (1989), Watson (1996), or in the present study. Larvae of both these species are quite similar

to *A. flavidus*; however, we recommend a more detailed study of larval *U. sanctaerosae* and *X. fucorum*, including a description of caudal skeleton development, before concluding that larval characters do, or do not, support Yatsu's (1985) classification. In particular, it would be interesting to investigate whether either species develops a fourth epural that fuses with the third, or a first epural that fuses with the neural spine of the second preural centrum during flexion. In another cleared and stained individual we observed fusion of the neural spines on the third and fourth preural centra (NPU4 and NPU3, Fig. 3D). However, only one specimen of *A. flavidus* was examined at each of these fusions and more specimens, when available, should be cleared and stained to determine if these fusions occur in all larval *A. flavidus*. Presence or absence of a ventral caudal radial may also be of interest. Although it is unclear what becomes of the ventral caudal radial between postflexion and juvenile stages from our study of *A. flavidus*, we hypothesize that it fuses with the tip of the haemal spine of the second preural centrum. Taking all of these unusual aspects of *A. flavidus* larval development into account, we suggest that development of *U. sanctaerosae* and *X. fucorum* should be further investigated to clarify the systematic relationships among the genera.

Acknowledgments

The authors thank Theodore Pietsch (University of Washington [UW]) for his help, support, and encouragement with this project. Beverly Vinter illustrated the specimens in the developmental series. We also thank the Ichthyoplankton Laboratory of the Alaska Fishery Science Center (AFSC) and the UW Fish Collection for use of their facilities and specimens. Ann Matarese (AFSC) and William Watson (NOAA-Southwest Fisheries Science Center) reviewed an earlier draft of the manuscript.

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Spatial and temporal patterns in the bycatch of seabirds in the Argentinian longline fishery

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Longline fisheries have grown throughout the world's oceans for more than 40 years. This type of fisheries has captured high-quality fish (mature individuals rather than unwanted juveniles), has had minimal destructive effects on bottom habitats, and has produced a low bycatch of nontargeted fish (Brothers et al., 1999). Seabirds, however, are hooked accidentally when they swallow or are snagged on the baited hooks set by commercial longline crews (Brothers, 1991; Barnes et al., 1997; Tasker et al., 2000; Belda and Sanchez 2001; Jahncke et al., 2001).

Population declines of several species of albatrosses and petrels in the Southern Ocean are linked to longlining operations (Croxall and Prince, 1990; Brothers, 1991; Cherel et al., 1996). The importance of the Patagonian shelf waters as a foraging habitat for seabirds is well documented (Cooke and Mills, 1972; Veit, 1995), particularly for black-browed albatross (*Thalassarche melanophris*; Gales, 1998). We estimated the magnitude of seabird mortality in the kingclip (*Genypterus blacodes*) fishery in the Argentine Exclusive Economic Zone (EEZ).

Materials and methods

Description of the fishery

Demersal longline vessels target two species on the Patagonian shelf of Argentina: kingclip and Patagonian toothfish (*Dissostichus eleginoides*). Six vessels operate within Argentina's EEZ in the South Atlantic: three vessels, *Marunaka*, *Estela*, and *Magallanes II*, fish mainly kingclip off Comodoro Rivadavia and Puerto Deseado and three vessels, *Antarctic I*, *II* and *III*, target Patagonian toothfish off Ushuaia. Another twelve vessels based in the Malvinas (Falkland) Islands and operating outside Argentina's jurisdiction target kingclip and Patagonian toothfish (Blake, 2001; Fig. 1). Within Argentina's EEZ, an artisanal longline fleet of 70 vessels target hake (*Merluccius hubbsi*), fishing mainly in shallower waters within the San Matias Gulf.

The kingclip fishery operates year round with trips lasting up to 65 days. Vessels are equipped with an autoline system; the line is 10 km in length and has up to 20,000 hooks which are baited with thawed squid at night by using a baiting machine. Offal is released strategically to attract birds to the opposite side of the vessel away from the main line during hauling.

Data collection

Observers, trained in seabird identification and in quantifying mortality, estimated fishing effort and the bycatch of seabirds. Data were collected through a special agreement between a fishing company (Argenova S.A.) and the university (Universidad Nacional de la Patagonia Austral). Observers sampled 156 sets and hauls from December 2000 to September 2001. Sets were deployed as early as 23:00 and as late as 04:00. Observers recorded the date, number of hooks deployed, position and time of the start and end of each set, water depth, and sea condition. If a bird was caught, or if we observed flapping wings or the struggle of a bird, we recorded the event. During hauling we identified and counted all drowned birds. We collected a sample of drowned birds and brought them to the laboratory to determine their sex. Observers sampled the sets of one of the three vessels targeting kingclip in Argentina's EEZ. We estimated total bird catch using observed bycatch and official information, such us the number of hooks deployed from logsheets of the other vessels.

Data analysis

We used the bootstrapping method to calculate the 95% confidence limits for the mean number of birds caught/1000 hooks and made 10,000 simulations (n=156). Using logistic regression, we determined which variables best explained the "capture events." Initial independent variables included date, number of hooks deployed, water depth, latitude, sea condition, time at which the setting began, and moon phase. Moon phase was scored from 0 to 14, where 0 represents a full moon and 14, a new moon. To determine the contribution of each variable to seabird mortality rates, we used a stepwise multiple regression (Zar, 1984). On sets with catch per unit of effort (CPUE) greater than 0, three separate multiple regressions were performed: 1) for total seabirds, 2) for albatrosses, and 3) for petrels. Seabirds whose sex was determined were used to test differences from the 1:1 sex ratio by using a χ^2 test (Zar, 1984). We compared, using this test, the number of birds of each species caught during winter, summer and autumn (Zar, 1984).

Manuscript submitted 28 May 2003
to the Scientific Editor's Office.

Manuscript approved for publication
24 October 2005 by the Scientific Editor.

Fish. Bull. 104:482–485 (2006).

Results

Bycatch of fish and seabirds

The mean depth for longlining operations was 139 ±11 meters (n=156) and the mean number of hooks per set was 20,474 ±2588 (n=156). Effort for the whole fleet during the nine-month sampling period represented a total of 10,088,235 hooks.

Kingclip represented 80% of the fish caught. Additional catch included Patagonian toothfish (2%), Argentine hake (3%; *Merluccius hubbsi*), Brazilian codling (8%; *Urophycis brasiliensis*), blackbelly rosefish (2%; *Helicolenus dactylopterus lahillei*), skates (5%; *Raja* spp.) and other fish in proportions below 1% (i.e., Patagonian cod (*Salilota australis*); hoki (*Macrorunus magellanicus*); tope shark (*Galeorhinus galena*), Patagonian smoothhound (*Mustelus schmitti*), among others).

Only two species of seabirds were caught during setting of the longline: 12 white-chinned petrels (*Procellaria aequinoctialis*) and 19 black-browed albatrosses; no seabirds were caught during hauling. Most fishing and bycatch occurred between 48–46°S latitude and 63–61°W longitude (Fig. 1). The observed distribution of genders was not significantly different from an expected 1:1 sex ratio for albatrosses (χ^2=0.06, df=1), or petrels (χ^2=0.15, df =1). Fifty-three percent of the albatrosses caught were males and 47% females (n=17). White-chinned petrel were evenly divided: 50% were males and 50% females (n=12). Bycatch was not homogenous throughout the year. The majority of the petrels were caught during autumn (χ^2=66.3, df=2, P<0.001), whereas albatrosses were predominantly caught during winter (χ^2=54.7, df=2, P>0.001, Fig. 2). We estimated a mean bycatch rate of 0.034 ±0.009 birds/1000 hooks which, extrapolated to the other vessels, represents a total of 343 birds caught in a nine-month period. Of these birds, 55% would be black-browed albatross and 45% white-chinned petrels.

Figure 1

Map showing ports (solid triangles) used by longliners in Argentina. Open triangles indicate set positions where seabird bycatch occurred and circles indicate sets without seabird bycatch. The 200-m isobath indicates the shelf break.

Factors affecting bycatch rates

Logistic regression analysis indicated that water depth (β_0=−0.96) and moon phase (β_0=0.24) explained most of the variability in "capture events"; the probability of a bird getting caught increased with water depth and during brighter nights. Two variables were important in explaining the variation in bycatch rate (F=3.13; df=4, 42; P=0.02): moon phase (β=−0.327, P=0.03) and water depth (β=0.335, P=0.02). When we analyzed the variables that explained the incidental capture for both species separately, moonlight was the most important for albatrosses (F=4.637, df=3, 21, β=−0.52, P<0.01), whereas water depth was the most important for petrels (F=2.4, df=2, 22, β=0.584, P<0.05).

Discussion

This note reports the first estimation of seabird bycatch in the Argentinean EEZ outside of the CCMLAR (Commission for the Conservation of Antarctic Marine Living Resources) area for the Atlantic Ocean with data from onboard observers. Pelagic seabird species, such as white-chinned petrels and black-browed albatrosses, actively forage in the highly productive Patagonian shelf waters (Cherel and Klages, 1998; Prince et al., 1998; Weimerskirch et al., 1999; Grémillet et al., 2000); therefore these species are especially vulnerable to fisheries around coastal shelf-edge habitats (Weimerskirch et al., 1999; Grémillet et al., 2000). These two species are often associated (Veit, 1995) and are similarly affected by longline fishing (Moreno et al., 1996; Berrow et al., 2000). We found the average bycatch rate to be 0.034 birds/1000 hooks, which is one or two orders of magnitude lower than those reported from other longline

fisheries in the South Atlantic (i.e., Brazil 0.126 birds/1000 hooks; [Neves and Olmos, 1998], Uruguay 4.7 birds/1000 hooks; [Stagi et al., 1998]), but similar to those reported for the CCAMLR region (1998: 0.025 birds/1000 hooks; 1999: 0.07 birds/1000 hooks; 2000: 0.0014 birds/1000 hooks; [Robertson et al., 2001]).

We made bycatch estimations from vessels, while voluntarily using mitigation measures to reduce fishery-induced mortality on seabirds—such as tossing thawed bait (less bouyant than frozen bait), setting lines only at night, and splashing the net buoys when birds came near the line. In a nine-month period, 343 seabirds were incidentally caught by vessels targeting kingclip, representing an annual mortality estimate of 457 birds. Previous crude estimations made for day-setting were considerably higher (2 birds/1000 hooks, Gandini and Frere, 2001).

The main factor affecting seabird mortality was water depth, which is directly related to the location of the setting because water depth increases towards the shelf break, where white-chinned petrels forage actively throughout the year (Weimerskirch et al., 1999; Berrow et al., 2000). Sixty-five percent of the birds were caught between five days after or before the full moon. A full moon affected albatrossess more significantly than it did petrels. Albatrosses forage mainly during the day, whereas white-chinned petrels forage both at night and during the day (Weimerskirch et al., 1999). Our results support the theory that darkness reduces seabird bycatch. Therefore, improving mitigation measures (i.e., using streamer lines, splashing bouys, etc.), during full moon phases, may reduce bird bycatch further. Birds were more susceptible to being caught in autumn and winter. Our findings agree with those of White et al. (2001), who mentioned that vulnerability for seabirds in Patagonian shelf waters is higher between September and June than during the rest of the year.

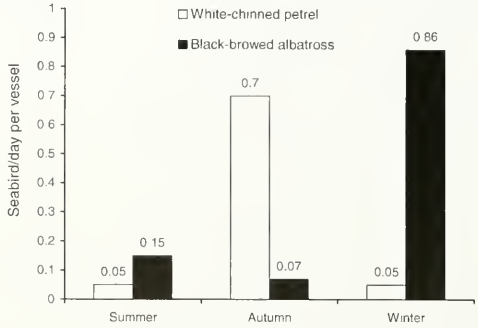

Figure 2

Bycatch rates for black-browed albatross *(Thalassarche melanophris)* and white-chinned petrels *(Procellaria aequinoctialis)* incidentally killed in longline fishery operations in Argentinian waters.

Population impacts and recommendations to reduce bycatch of seabirds

At least 500,000 pairs (nearly 86% of the world population) of black-browed albatrosses breed on the Malvinas and Falkland Islands and forage on the highly productive Patagonian shelf. Thus, the black-browed albatross catch estimated in this study represents <1% of the total population. Similarly, the world population of white-chinned petrels is estimated at more than a millon breeding pairs (Croxall et al., 1984; Woods and Woods, 1997); therefore, less than 1% of the white-chinned petrel population is removed by longlining each year. Although these estimates may not seem to be critical for the affected species, they may be more significant than indicated because even a small increase in long-lived species may cause populations to decline. Moreover, the lack of information on seabird bycatch by illegal, unreported, and unregulated fishing, make the overall population-level impact from bycatch not only difficult to assess but likely much higher than currently realized. Estimations of seabird bycatch by illegal fleets range from 7000–15,000 albatrosses and 1200–2000 petrels killed during 2000 (Baird, 2001). These figures are almost seven times larger than our estimates for the Argentinian kingclip fleet operating in the south Atlantic.

Our data indicate that collaboration between fisherman and technicians to find devices that reduce bait loss and that improve fish CPUE for practical application (no additional actions to be taken during fisheries operations) is likely critical to maintaining seabird populations. We recommend offering financial benefits to fishing crews that catch fewer seabirds and offering appropriate fishing gear and incentives for compliance in order to reduce seabird bycatch in the Atlantic Ocean.

Acknowledgments

We are indebted to Diego Brigatti who provided valuable assistance with the vessels, to Julián Crugeiras from ARGENOVA SA fishing company, and to Eric Gilman and Dee Boersma for their critical comments on an earlier version of this note. This study was carried out with financial support from the Wildlife Conservation Society, Jeniam Fundation, Fish and Wildlife Service, and Universidad Nacional de la Patagonia Austral.

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Volume 104
Number 4
October 2006

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Periodicals postage is paid at Seattle, WA. POSTMASTER: Send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn.: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

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The Secretary of Commerce has determined that the publication of this periodical is necessary according to law for the transaction of public business of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $55.00 domestic and $68.75 foreign. Cost per single issue: $28.00 domestic and $35.00 foreign. **See back for order form.**

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U.S. Department of Commerce
Seattle, Washington

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Number 4
October 2006

Fishery Bulletin

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Geographical differences in the feeding patterns of red rockfish (*Sebastes capensis*) along South American coasts

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Abstract—Feeding habits and feeding strategy of red rockfish (*Sebastes capensis*) were studied from fish captured along most of the range of this species in coastal waters of South America. Stomach contents of 613 individuals, collected during 2003, were analyzed. Fish were obtained from six locations along the Chilean (23°S to 46°S) and Argentinian (43°S) coasts. The main prey items were Mysidacea (75.06% IRI), Osteichthyes (6.29% IRI),and *Rhynchocinetes typus* (6.03% IRI). Predator sex and size did not significantly affect the diet, but significant differences were found between locations. Four geographical areas, discriminated by prey occurrence and frequencies, were determined: three on the Pacific coast and one on the Atlantic coast. These areas correspond roughly with biogeographic zones described for the Chilean and southern Argentinian coasts. The feeding strategy index (FSI) indicated a specialized feeding strategy for *S. capensis* for most of its range. However, the FSI does not include the behaviour of a predator, and the FSI must be interpreted carefully for fishes like *S. capensis* that are passive ambush feeders. The abundance and availability of different prey may explain both the geographic differences in dietary composition and the specialized feeding strategy of *S. capensis*.

Manuscript submitted 18 November 2004 to the Scientific Editor's Office.

Manuscript approved for publication 1 November 2005 by the Scientific Editor.

Fish. Bull. 104:489–497 (2006).

The feeding habits of a species, determined by its physiological, and behavioral adaptations, form a basic aspect of its biology; they provide a way to understand the trophic interactions between predators and their prey (Herrán[1]). Throughout the evolution of behavior and morphological adaptation there have been strong selective pressures toward those characteristics that allow a species to capture its prey and to escape from predators (Hixon and Beets, 1993; Reznick et al., 1997; Abrams, 2000).

Most trophic studies in fishes are carried out only on a local scale (e.g., Moreno and Zamorano, 1980; Ojeda and Fariña, 1996), and rarely consider the predator's entire distributional range. Thus, conclusions about the species' trophic patterns can reflect local conditions rather than a generalized feeding habit. In the Southern Hemisphere, red rockfish (*Sebastes capensis* (Gmelin, 1788)) is the only known species within this genus. It is distributed from the Pacific coast (the coast of Peru and Chile), to east of the Falkland Islands, to east of Tristan da Cunha, and as far as the southwestern coast of South Africa (Chen, 1971; Kong, 1985). *Sebastes capensis* is an ovoviviparous species that inhabits the waters over the continental shelf between 20 and 200 m in depth (Pequeño, 2000). Despite the economic importance of this species along the north and central coast of Chile, where it is exploited by local fisherman, there is little information about its biology and ecology. Currently, there is only one known study describing the diet of this species from the central Chilean coast (Ojeda and Fariña, 1996).

In our study, the feeding habits of *S. capensis* are described and its feeding strategy is analyzed along its geographic range in South America in order to understand whether the feeding pattern and the trophic behavior of this species are maintained at the regional scale. Moreover, the ability of the feeding strategy index of Amundsen et al. (1996) is evaluated for a predator like *S. capensis* that is a passive ambush feeder.

Materials and methods

Sampling

The area of study included most of the distributional range for *S. capensis* (Fig. 1) along the Chilean coast—Antofagasta (23°11′S; 70°29′W), Coquimbo (29°58′S;71°19′W), Val-

[1] Herrán, R. A. 1988. Stomach contents in fishes: bibliographic revision of objectives and methods. Technical report of the Instituto Oceanográfico Español, number 63, 74 p. Muelle de Poniente s/n; Apartado 291; 07015 Palma de Mallorca; Islas Baleares; Spain. [In Spanish.]

paraíso (32°54′S; 71°44′W), Talcahuano (36°44′S; 73°07′W), Valdivia (39°45′S; 73°08′W), and Aysén Fjord (45°34′S; 72°05′W—and in the Golfo Nuevo (42°45′S; 65°01′W) on the Argentinian coast.

Fish were captured between April and November of 2003. Details for each sampling period in each location are given in Table 1. The depths of capture varied from 15 to 50 m. Fish were captured 1) with hand lines from artisanal boats, 2) by submarine divers, or 3) they were acquired from local fishermen. Overall, a total of 613 specimens were analyzed, of which 375 were males and 238 were females.

Laboratory analysis

Immediately upon being captured, the fish were transferred from the sampling location to the laboratory, where they were frozen until analysis. The total length (TL) of each fish was measured to the nearest 1 cm of precision, total weight was recorded to the nearest 0.5 g precision), and sex was determined by macroscopic observation of the gonads.

The prey items found in the stomachs were sorted, counted, weighed, and identified to the lowest possible taxonomic level, according to Holthuis,[2] Garth,[3] Holmquist,[4] and Retamal (1981) for crustaceans, and according to Moreno and Castilla[5] for fishes.

Dietary analysis

Traditional methods of dietary analysis (counts, frequencies of occurrence, and weights of individual prey [Hyslop, 1980]) were used. These methods can either underestimate or overestimate the results. For this reason, a compound method of analysis was used. One of the most widely used compound indices in fish diet studies is the index of relative importance, IRI (Pinkas et al., 1971), which is expressed as a percentage, % IRI (Cortés, 1997). This index was calculated at the species and phylum level.

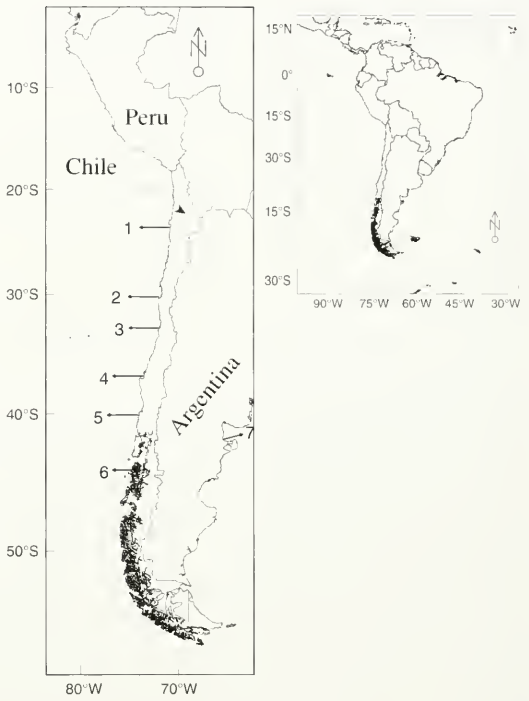

Figure 1

Sampling locations for red rockfish (*Sebastes capensis*) along the Chilean and Argentinian coasts. 1=Antofagasta, 2=Coquimbo, 3=Valparaiso, 4=Talcahuano, 5=Valdivia, 6=Aysen, and 7=Golfo Nuevo (Argentina).

Feeding strategy

The analysis of dietary composition proposed by Amundsen et al. (1996) was used.

This is based on a graphic representation; prey-specific abundance is plotted against the prey's frequency of occurrence on a two-dimensional space:

$$Pi = \frac{\sum Si}{\sum Sti} \times 100,$$

where Pi = the prey-specific abundance of prey i;
Si = the stomach contents (by weight) comprising prey i; and
S_{ti} = the total stomach contents (by weight) in only those predators with prey i in their stomachs.

This index gives information about prey importance (dominant versus rare) and the feeding strategy (gen-

[2] Holthuis, L. 1952. The Crustacea Decapoda Macrura of Chile. Reports of the Lund University Expedition 1948–49. Lunds Universitets Arsskrift 247(10):1–110. Lunds Universitets, Lund, Sweden.

[3] Garth, J. 1957. The Crustacea Decapoda Brachyura of Chile. Reports of the Lund University Expedition 1948–49. Lunds Universitets Arsskrift. number 7, 125 p. Lunds Universitets, Lund, Sweden.

[4] Holmquist, C. 1957. Mysidacea of Chile. Reports of the Lund University Expedition 1948–49. Lunds Universitets Arsskrift. number 6, 52 p. Lunds Universitets, Lund, Sweden.

[5] Moreno, C., and J. Castilla. 1978. Guide for the recognition and observation of fish from Chile. Expedition of Chile, 120 p. Universidad Austral de Chile, Casilla 567-Isla Teja, Valdivia, Chile. [In Spanish.]

Table 1

Sampling period and mean sizes (mean, in cm) of red rockfish (*Sebastes capensis*) examined by location and latitude. n=number of stomachs with prey; SD=size standard deviation, and P=probability associated with Kruskal-Wallis test. ns=no significant differences.

				Total length		
Location	Latitude	Sampling period	n	Mean	SD	P
Antofagasta	24°S	May–June 2003	29	24.8	1.74	ns
Coquimbo	30°S	May 2003	21	26.2	4.39	ns
Valparaiso	33°S	April–May 2003	50	22.2	3.02	ns
Talcahuano	36°S	April–May 2003	59	26.8	1.66	<0.05
Valdivia	40°S	April–May 2003	87	26.2	3.34	<0.05
Aysen fjord	45°S	July, November 2003	25	25.1	2.15	ns
Golfo Nuevo	43°S	June 2003	23	27.1	2.60	ns

eralist versus specialist) of the predator. The vertical axis of a hypothetical index represents the feeding strategy of the predator in terms of specialization or generalization. Prey points located at the upper left of the diagram would be indicative of specialization of individual predators, and those in the upper right would represent specialization of the predator population. Data seen in the upper right of the diagram (population specialization) necessarily restricted to a single point or to a few points, would reflect a predator population with a narrow niche diet. If all prey points were located along or below the diagonal from the upper left to the lower right, the predator population would have a broad niche width. Prey points located in either the upper left or the lower right corner would represent prey that make the same overall contributions to the population diet, but they would be indicative of totally different feeding strategies for the individual predators. Prey with high specific abundance and low occurrence (upper left) would be consumed by a few individuals displaying specialization, whereas prey with a low specific abundance and a high occurrence (lower right) would be eaten occasionally by most individuals. These differences in feeding strategy are related to the between- and within-phenotypic contributions to the niche width. In a population with a high between-phenotypic component, individuals specialize on different resource types. In a population with a high within-phenotype component, most of the individuals use many resource types simultaneously.

Statistical analysis

The Mann Whitney test was used to compare the sizes of fish between sexes, and the Kruskal-Wallis test was performed to compare the sizes of fish from different locations (Zar, 1999). The χ^2 contingency tables were used to evaluate the possible differences in the prey items clustered by phylum (Arthropoda, Chordata, and Mollusca) among locations. In addition, the G-statistic was used to evaluate differences in the occurrences of different prey types between sexes (Zar, 1999) and among the different size classes of fish defined arbitrary (class 1: fish between 18 and 25 cm, and class 2: fish between 26 and 38 cm) (Zar, 1999).

A correspondence analysis was used to evaluate the association between occurrences of prey items and the different locations, allowing the ordination of samples in a reduced space (two dimensions) (Digby and Kempton, 1987).

Results

Fish characteristics

A total of 613 specimens were analyzed and of those 296 stomachs contained some prey, 189 had empty stomachs, and 128 had everted stomachs (48.29%, 30.83% and 20.88%, respectively). Table 1 summarizes the characteristics of the fish analyzed by location. There was no significant difference in body size between males and females (U=9854.5, P=0.26). The size of fish differed significantly among locations: fish from Talcahuano and Valdivia did not differ significantly in size but were significantly larger than those from the others locations (Table 1).

Diet analysis

Across the geographical range, a total of 60 prey items were identified (Table 2): 40 crustaceans, 9 fishes, 3 cephalopods, 7 snails, and 1 polychetes. Crustaceans were the predominant prey in the diet of *S. capensis*. The low occurrence of other prey items allowed us to designate this species as carcinophagous (=feeding mainly on crustaceans).

Overall, the most important prey item was Mysidacea unident. (75.06% IRI), followed by Osteichthyes unident. (6.29% IRI), the rock shrimp *Rhynchocinetes typus* (6.03% IRI), deep red crab (*Petrolisthes desmarestii*) (4.67 % IRI), the rock crab *Cancer setosus* (2.32%

Table 2

Index of relative importance (IRI %) of each prey item recorded by location. Bold numbers show the most important prey items in each location. ANF=Antofagasta; COQ=Coquimbo; VAP=Valparaiso; THN= Talcahuano; VAD=Valdivia; AYS=Aysen channels; GNU=Golfo Nuevo. Unid.=unidentified.

Item prey	ANF	COQ	VAP	THN	VAD	AYS	GNU
Phylum Arthropoda							
Class Crustacea							
Rhynchocinetes typus	**40.76**	**92.15**	**27.38**	0.08			
Cancer setosus	1.17	0.17	**34.32**	5.09	0.19		
Cancer edwarsi				0.31			
Petrolisthes desmarestii	**48.68**	1.03	19.09	6.40			
Petrolisthes tuberculosus					0.29		
Pilumnoides perlatus	0.88	0.20	0.19	3.80	0.21		
Pagurus sp.		0.17					
Paguristes sp.				0.01			
Pagurus edwarsi			0.19		0.01		
Pagurus villosus						0.07	
Eurypanopeus crenatus					0.06		
Pseudocorystes sicarius						**94.63**	
Eurypodius latreillei				3.69	0.06		
Gaudichaudia gaudichaudi			0.46	0.01			
Taliepus sp.			0.21				
Pachycheles chubutensis							0.50
Pisoides edwardsi			0.25				
Pinnixa sp.						0.19	
Pterygosquilla armata		0.22			0.41		
Munida gregaria							**15.84**
Munida subrugosa							**32.07**
Halicarcinus planatus			0.65				**23.53**
Betaeus sp.	0..23						
Bateaus truncatus				**6.97**	0.04		
Synalpheus spinifrons	4.01		0.65				
Nauticaris magellanica			0.60	0.10	0.02		
Pleuroncodes monodon				0.04			
Austrapandalus grayi				0.04			
Exosphaeroma sp.							0.29
Mysidacea unid.				**71.94**	**92.13**		
Amphipoda unid.				0.05	0.005		
Euphausiacea unid.					0.002		
Alpheidae unid.				0.01			
Cirolanidae unid.							1.17
Porcellanidae unid.			0.23				
Cirripedia unid.				0.01			
Decapoda unid.		0.22					
Macruridae unid.			2.60	0.67	0.002	0.90	0.79
Braquiuridae unid.			0.65	0.61			

continued

Table 2 (continued)

Item prey	ANF	COQ	VAP	THN	VAD	AYS	GNU
Phylum Chordata							
Class Osteichthyes							
Engraulis ringens	0.52				0.37		
Chromis crusma		**3.54**		0.01			
Helcogramoides cumungamii					0.10		
Hipsoblennius sordidus					0.04		
Merluccius gayi				0.09			
Normanichthyes crokeri					0.06		
Odonthestes regia			0.25	0.01	0.36		
Osteichthyes unid.	1.25	2.12	8.49	0.03	**5.49**	**4.15**	**22.47**
Scorpaeniformes unid.					0.09		
Phylum Mollusca							
Class Cephalopoda							
Enteroctopus megalocyathus							0.74
Robsonella fontaniana			1.01				
Teuthoidea unid.					0.01		
Class Gastropoda							
Bittium peruvianum					0.002		
Turritella cingulata			2.60				
Nassarius dentifer	0.88						
Nassarius gayi	1.42						
Nassarius sp.		0.17					
Tricolia sp.				0.01	0.05		
Gastropoda unid.						0.03	1.17
Phylum Annelida							
Class Polychaeta							
Polychaetae unid.	0.21		0.19	0.03	0.002	0.03	1.19

IRI), and the megalop larvae of *Pseudocorystes sicarius* (1.78% IRI).

At the phylum level, the IRIs indicated that the most important prey group was Arthropoda (96.6%) followed by Chordata (2.93%), Mollusca (0.07%), and a low representation of Annelida (0.029%).

There were no differences between the sexes in the diet of *S. capensis*. Males and females both ate similar proportions of prey items (G=3.3; P>0.05). Neither sex was observed to show ontogenetic dietary changes: fish of the 19–25 cm size class, and fish between 26 and 38 cm TL showed no significant differences in prey items (G=2.27; P>0.05). On the other hand, there were significant differences in the diet of *S. capensis* among locations (χ^2=44.94, P<0.05). The correspondence analysis (Fig. 2) indicated that fish from Antofagasta, Coquimbo, and Valparaíso fed on similar prey items; whereas the fishes from Talcahuano and Valdivia fed mainly on other prey (Mysidacea spp.). Fish from the Aysén channels and the Argentinia coast showed qualitatively different diets. The diet of fish from the Aysén channels was characterized by the absence of those prey (e.g., *R. typus; P. desmarestii*) recorded in the fish from the northern locations. On the other hand, fish from the Argentina coast, fed on prey that are distributed only in higher latitudes (e.g., *Munida* spp.).

Table 2 summarizes the IRI % for each prey item in each location.

Antofagasta In this location, 29 specimens had stomach contents, from which 13 prey items were identified. The most important prey was the crab *P. desmarestii* (48.68% IRI), followed by the rock shrimp, *R. typus* (40.76% IRI), and low occurrences of shrimp *Synalpheus spinifrons* (4.01% IRI) and rock crab *C. setosus* (1.17% IRI).

Coquimbo Only 10 types of prey were identified from this location. The most predominant was *R. typus* (92.15%

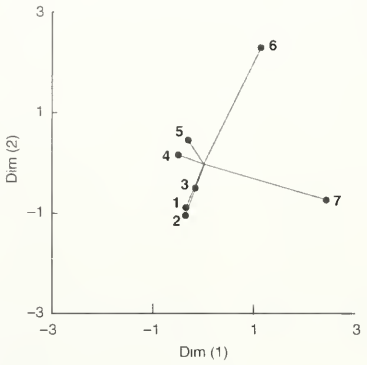

Figure 2

Compositional gradients of correspondence analysis of prey items (shown in Table 1) by location. 1=Antofagasta, 2=Coquimbo, 3 =Valparaíso, 4=Talcahuano, 5=Valdivia, 6=Aysen, and 7=Golfo Nuevo (Argentina). Dim (1)=dimension 1; Dim (2)=dimension 2.

IRI), followed by the fish *Chromis crusma* (3.54 % IRI) and unidentified Osteichthyes (2.12 % IRI). Polychaetes were not found in this area, and only one type of prey belonging to the phylum Mollusca was recorded.

Valparaíso Nineteen prey items were identified; of those, 14 were crustaceans. In this location, three prey items were predominant: the crab *C. setosus* (34.32% IRI), the shrimp, *R. typus* (27.38% IRI), and the crab, *P. desmarestii* (19.09% IRI). The fishes were relatively well represented (unidentified Osteichthyes 8.49% IRI). The Mollusca (2.60% IRI) were represented by the small octopus *Robsonella fontaniana,* and the snail *Turritella cingulata.*

Talcahuano A total of 24 prey items were identified from this location: 18 crustaceans, four fishes, one snail, and one polychaetae. The most important prey item was Mysidacea spp. (70.94% IRI), followed in importance by the crabs *P. desmarestii* (6.4% IRI) and *C. setosus* (5.09% IRI).

Valdivia Twenty four prey items were identified from this area. Mysidacea spp. was the most important in this location (92.13% IRI). However, six of the fish species we identified were represented in this area.

Aysén Fjord Despite the importance of unidentified prey items in this area, we observed an absence of most of the prey items found in the other locations. However, the trend of the predominance of crustaceans continued. The most important prey item was the megalop of *P. sicarius* (94% IRI) and unidentified Osteichthyes (4.15%). The larval stage of *P. sicarius* occurs seasonally; therefore, their importance in the diet of *S. capensis* from this geographical area can be associated with the sampling period (November).

Golfo Nuevo In this area, 12 prey items were identified. Lobster krill *Munida subrugosa* (32.07% IRI), the brachyuran crab *Halicarcinus planatus* (23.53% IRI), and *Munida gregaria* (15.84% IRI) were the most important prey items. The percentage of unidentified Osteichthyes (22.47% IRI) was higher than in other locations on the Chilean coast.

Feeding strategy

Figure 3 shows prey-specific abundance plotted against frequency of occurrence of prey items for *S. capensis* in the entire study area (Fig. 3A), and in each subarea (termed "location" in this article) (Fig. 3, B–H). This pattern of point distributions was similar for almost all locations. Most of the points (frequency of occurrence) were close to the left side of the *x* axis, and they tended to be positioned towards the upper left corner of the graph (specific abundance). There was a high between-phenotype contribution (BPC) to the niche width in Antofagasta (3B), Coquimbo (3C), Valparaíso (3D), Aysén fjord (3G), and Golfo Nuevo(3H) (i.e., individual predators specialized on different prey types and each food category was consumed by only a limited fraction of the predators). A more mixed feeding strategy, with varying degrees of specialization and generalization for different prey types was observed in Talcahuano (3E) and Valdivia (3F) (i.e., a high BPC and lower within-phenotype contribution (WPC) to the niche width). On the other hand, predominant prey items were observed only in Coquimbo, Valdivia, and Aysén fjord (*R. typus*, Mysidacea gen. sp., and the megalops of *P. sicarius,* respectively); rare or occasional prey items (crustaceans, fishes, mollusks, and polychaetes) were found in all locations.

Discussion

To determine the dietary variability of a predator, in order to describe its feeding pattern over its entire geographical range, is a difficult task because of the need for large sample sizes in a number of locations. Additionally, fish, such as *S. capensis*, whose percentages of empty or everted stomachs are high (50%), make an assessment of diet variability yet more difficult. We managed these difficulties by sampling fish during the same season, sampling over a similar depth range, and by using known information about the geographical distribution of prey items.

Geographical variation in the diet

The high percentage of crustaceans in the diet of *S. capensis* indicates that is primarily a carcinophagous fish,

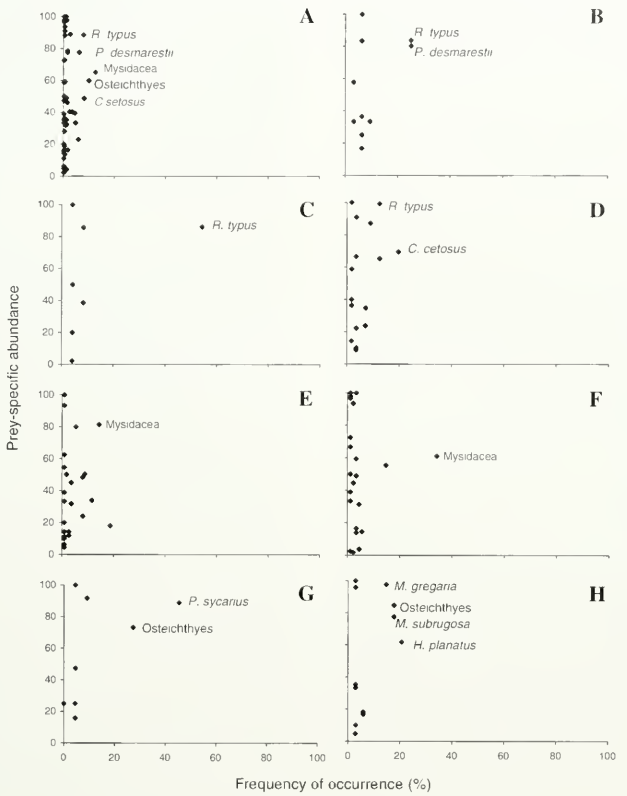

Figure 3

Prey-specific abundance (Pi) plotted against frequency of occurrence (%F) of prey items for red rockfish (*Sebastes capensis*) from the Chilean and Argentinean coasts. (**A**) entire geographic area, (**B**) Antofagasta, (**C**) Coquimbo, (**D**) Valparaíso, (**E**) Talcahuano, (**F**) Valdivia, (**G**) Aysen Fjord, and (**H**) Golfo Nuevo. *R. typus*= the rock shrimp *Rhynchocinetes typus*; *P. desmarestii*=deep red crab (*Petralisthes desmarestii*); *C. setasus*=the rock crab *Cancer setosus; M. gregraria*=the lobster krill *Munida gregaria; M. subrugosa*=the lobster krill *Munida subrugosa; H. planatus*=the brachyuran crab *Halicarcinus planatus.*

and secondarily, a piscivorous species. Sixty prey items were recorded in the entire study area, including Mysidacea (75.06% IRI), the most important prey, followed by Osteichthyes (6.29% IIR), *Rhynchocinetes typus* (6.03% IRI), and *Petrolisthes desmarestii* (4.67% IRI).

The composition of prey species for *S. capensis* showed clear geographic variation. These changes were reflected by the relative importance of the different prey items in each of the study locations (Table 2) and were most evident in the fjords of Aysén and on the Argentinian coast, where all of the prey items found (except for *Halicarcinus planatus*) were unique to those locations. The crustacean *R. typus* was one of the most important prey items (50% IRI) between 23°S and 33°S. The rock shrimp *R. typus* is distributed from 10°S in Perú to 38°S on the Chilean coast (Retamal, 1981). Therefore, this prey species is not available on the southern Chilean coast (southward from 38°S). Between 37°S and 40°S,

Mysidacea was the most important prey item. In this geographic area, the mysids are also the most important prey item for other rocky bottom fishes (González and Oyarzún, 2003). Mysids are found in large and dense patches a few centimeters from the benthos (Silva and Stuardo, 1985).

The changes in prey types and their differences in IRI were also supported by a correspondence analysis (Fig. 2), which separated the sampling locations into four major areas according to recorded prey types as follows: 1) 23°S–33°S, 2) 37°S–40°S, 3) 45°S, and 4) Golfo Nuevo (43°S), Argentina. These geographic areas agree well with the proposed biogeographic units for this region by Briggs (1995) and by Camus (2001). According to Briggs (1995), two faunistic provinces are recognized in the southeastern Pacific: the Peruvian province, which extends from Perú (ca. 10°S) down to the northern Chilean coast (ca. 30°S), and the Magellanic province located on the southern Chilean coast (ca. 43°S). Between these provinces a transitional zone is found, in which species typical of the Peruvian province and the Magellanic province overlap (Brattström and Johanssen, 1983; Lancelloti and Vasquez, 2000). Additionally, Camus (2001) recognized five areas of distributional discontinuities along the Chilean coast: (1) 30°S; (2) 33°S; (3) 37°–38° S; (4) 41°–43°S, and (5) 52°–53°S. Thus prey, such as *R. typus*, are distributed along the Peruvian province and transitional zone, whereas prey like mysids are present mainly between latitudes 37°S and 40°S.

Alternatively, Balech (1954) and Pequeño (2000) considered all of South America's southern extremity as the same biogeographic province. The records of prey items (i.e., *Munida gregaria* and *M. subrugosa*) in Golfo Nuevo (Argentina coast) support the existence of a connection between the southeastern Pacific and the southwestern Atlantic. These prey species are also distributed along the Chilean coast from Chiloé (42°S) southward. However, these prey items were not found in Aysén fjord, which could be explained by the presence of two zones in the Aysen area with different physical and faunistic conditions: the fjord channels and a marine zone (Arntz et al., 1999). Fish were sampled in the Aysen channels, where species of *Munida* are absent (Retamal, 1981). Therefore, abundance and availability of prey may be a factor explaining the differences in the dietary composition of *S. capensis* between biogeographical regions.

The present study indicates the existence of geographic variations in the dietary composition of *S. capensis*, and these variations generally agree with the zoogeographic limits proposed in the literature. However, the interpretation of this result is limited because of the absence of an adequate background on the abundance and biogeography of each prey item.

Feeding strategy

According to Ojeda and Fariña (1996), *S. capensis* is a nocturnal predator that feeds selectively on the decapod crustaceans *R. typus* and *P. perlatus* in the rocky subtidal shores of the central Chilean coast. Ojeda and Fariña suggested that these species are consumed preferentially from a large array of potentially abundant invertebrate prey items. Crustaceans are more active at night than during the day, which could explain their large rate of consumption by rockfishes that are active a night. Decapod crustaceans have the highest caloric content (Duarte et al., 1980), therefore Ojeda and Fariña (1996) proposed that the specialized diet of *S. capensis* reflects an optimal foraging alimentary strategy based on the maximization of available energy. On the other hand, Moreno and Zamorano (1980) indicated that the feeding strategy of a species has a direct relationship with its morphological and behavioral adaptations that preclude being preyed upon, and these adaptations could restrict the potential prey items that they could capture. In this context, Moreno et al. (1979) and Moreno (1981) studied the bathymetric distribution of six species of fishes from the rocky subtidal shore of the Valdivian coast, including *S. capensis*. They established that the fishes segregate by habitats in order to take refuge from predators, mainly the sea lion *Otaria flavescens*; such segregation was not related to the bathymetric distribution of their most important prey items.

Sebastes capensis shows buccal traits characteristic of carnivorous speciesl it has a good protrusion capacity and its teeth are inclined in a dorsal-caudal orientation that prevents the escape of prey once they have been caught (Alvarado, 1985). *Sebastes capensis* is a poor swimmer; its anatomy conforms to that of sedentary species in that its head and mouth are big in comparison to the rest of the body, and it has big eyes that allow an extensive angle of vision facilitating the capture of their prey and the detection of their predators. Therefore, their capacity to catch prey depends mainly on characteristics of their prey. All prey species of *S. capensis* show similar behavioral traits (i.e., swimming organisms that move between rocky intertidal and subtidal zones) and *S. capensis* waits to capture them. The specialized feeding strategy of *S. capensis* may be a consequence of the availability of prey species moving in the vicinity of the refuges of this fish.

The feeding strategy index, as defined by Amundsen et al. (1996), has been used successfully for active predators like sharks (e.g., Lucifora et al., 2000; Vogler et al. 2003). However, this index does not integrate either predator behavior or the availability of prey in a given environment. Therefore, the criteria used to differentiate specialist from generalist predators must be clarified. According to the feeding strategy index of Amundsen et al. (1996), *S. capensis* is a specialized predator (preying mainly on crustaceans, although it consumes some prey species, and other rare prey species in almost all locations analyzed). In reality, *S. capensis* is an ambush predator that does not actively search for its prey. Because this fish waits in rocky refuges for mobile prey, the probability of it encountering prey depends, to a large extent, on prey abundances, prey distributions, and prey behaviors.

Acknowledgments

The authors thank to Carlos Jara for the collaboration in the identification of crustaceans prey. This study was realized under the sponsorship of D.I.D. (Dirección de Investigación y Desarrollo) of the Universidad Austral de Chile (Project D-2003-09). M.T.G. was supported by a CONICYT fellowship of the Chilean Government.

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The use of otolith morphology to indicate the stock structure of common coral trout (*Plectropomus leopardus*) on the Great Barrier Reef, Australia

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Abstract—We investigated the use of otolith morphology to indicate the stock structure of an exploited serranid coral reef fish, *Plectropomus leopardus*, on the Great Barrier Reef (GBR), Australia. Otoliths were measured by traditional one- and two-dimensional measures (otolith length, width, area, perimeter, circularity, and rectangularity), as well as by Fourier analysis to capture the finer details of otolith shape. Variables were compared among four regions of the GBR separated by hundreds of kilometers, as well as among three reefs within each region, hundreds of meters to tens of kilometers apart. The temporal stability in otolith structure was examined by comparing two cohorts of fully recruited four-year-old *P. leopardus* collected two years before and two years after a significant disturbance in the southern parts of the GBR caused by a large tropical cyclone in March 1997. Results indicated the presence of at least two stocks of *P. leopardus*, although the structure of each stock varied depending on the cohort considered. The results highlight the importance of incorporating data from several years in studies using otolith morphology to discriminate temporary and possibly misleading signals from those that indicate persistent spatial structure in stocks. We conclude that otolith morphology can be used as an initial step to direct further research on groups of *P. leopardus* that have lived at least a part of their life in different environments.

Manuscript submitted 14 February 2005 to the Scientific Editor's Office.

Manuscript approved for publication 10 November 2005 by the Scientific Editor.

Fish. Bull. 104:498–511 (104).

Marine fish populations are generally distributed over large geographical ranges in a heterogeneous environment. Variable physical and biological processes may restrict the exchange of dispersive larvae and adults between areas within a population's species range, resulting in groups of individuals that are phenotypically or genetically distinguishable. Genetic and environmental processes may also have variable effects on the productive capacity (e.g., growth and reproduction) of individuals in different areas. Such variations may be directly measurable with variable life history characteristics, but also indirectly measurable with phenotypic characteristics, such as meristic and morphological characteristics.

Groups of individuals with different genetic or phenotypic characteristics can be defined as separate stocks. Although the precise definition of a stock has been widely debated (see reviews by MacLean and Evans, 1981; Begg, 1998; Booke, 1999), its ultimate meaning should depend on the management objective related to its use. If the management objective is to protect the genetic diversity of a species, for example, genetic information should be sought. If the purpose is to prevent over-fishing and localized depletion, information about life history characteristics is required. This information is needed because groups with different life history characteristics may respond differently to fishing pressure and therefore have different vulnerabilities to over-fishing (Cole, 1954; Adams, 1980; Jennings et al., 1998).

Variations in morphological characteristics of otoliths have proved useful for identifying stocks for a range of temperate marine fishes (e.g., Bird et al., 1986; Castonguay et al., 1991; Smith, 1992; Campana and Casselman, 1993; Friedland and Reddin, 1994; Begg et al., 2001; Smith et al., 2002), but have not been examined for tropical reef fishes. Differences in morphological characteristics between putative stocks indicate that the stocks have spent some periods of their lives in different environments (Begg et al., 1999; Cadrin, 2000) and therefore have the potential to develop different life history characteristics. Otolith morphological characteristics used as indicators of stock separation generally fall within one of three categories. The first category includes the traditional one-dimensional linear measurements of size-related attri-

butes, such as otolith length and width (e.g., Begg and Brown, 2000; Bolles and Begg, 2000) and distances between specific features on the otolith (e.g., Turan, 2000). Internal otolith measurements, such as nucleus length (e.g., Messeih, 1972; Neilson et al., 1985) and width of hyaline bands or increments (e.g., Begg et al., 2001) also fall within this category. The second category comprises two-dimensional size measurements, such as area, perimeter (e.g., Campana and Casselman, 1993; Begg and Brown, 2000; Bolles and Begg, 2000) and different shape indices, including circularity and rectangularity (e.g., Friedland and Reddin, 1994; Begg and Brown, 2000; Bolles and Begg 2000, Tuset et al., 2003). A third, more recent morphological technique examines the two-dimensional outline of otolith shape using Fourier analysis (e.g., Bird et al., 1986; Smith, 1992; Campana and Casselman, 1993; Begg and Brown, 2000; Smith et al., 2002). Fourier analysis produces a series of cosine and sine curves from the coordinates of a traced outline which, when added together, describe the outline of the traced form. The cosine and sine curves can be defined mathematically in a series of Fourier descriptors and used as variables to compare otolith shapes among individuals or potential stocks (Christopher and Waters, 1974; Younker and Ehrlich, 1977).

Plectropomus leopardus (common coral trout) (also known as leopard coralgrouper, FishBase[1]) is the most important commercially and recreationally harvested reef fish on the Great Barrier Reef (GBR), Australia (Mapstone et al.[2]; Williams[3]). *Plectropomus leopardus* comprises between 35% and 50% of the commercial reef line catch annually (Mapstone et al.[2]) and in 2004 a total allowable commercial catch (TACC) of 1300 t was implemented. Regional (hundreds of km) or inter-reef (hundreds to thousands of m) variations have been demonstrated in some life history characteristics of *P. leopardus* on the GBR (Begg et al., 2005), such as differences in density (Ayling et al.[4]), reproductive strategies (Adams, 2002), size and age (Russ et al., 1995; Lou et al., 2005), and mortality (Russ et al., 1995, 1998; Mapstone et al., 2004). Current management arrangements (such as TACC, fish size limits, gear restrictions, recreational bag limits, and spatial and temporal closures), however, do not incorporate the localized or regional spatial structure in the life history characteristics of *P. leopardus* or any other exploited species on the GBR.

The overall aim of this study therefore was to examine the use of otolith morphology for determining the stock structure of *P. leopardus* on the GBR. We investigated the broad spatial scale of *P. leopardus* by comparing aspects of otolith morphology among fish collected from four regions of the GBR, separated by hundreds of kilometers (north to south). Otolith structure was also assessed at finer spatial scales, among *P. leopardus* collected from neighboring reefs separated by hundreds of meters to tens of kilometers, within each of the four regions. In addition, because temporal variation in otolith shape could confound the spatial information if samples were taken from only one time, we also compared otolith morphological characteristics from two cohorts of *P. leopardus* with non-overlapping life histories either side of a significant environmental disturbance that affected the southern half of the GBR (the large and persistent Cyclone Justin in March 1997). Spatially variable effects of the Cyclone, such as a significant drop in temperature and salinity in large parts of the GBR (AIMS[5]), provided us with a unique opportunity to test the temporal stability of spatial patterns in otolith morphology.

Methods and data analysis

Background

Common coral trout (*Plectropomus leopardus*) were collected as part of the Cooperative Research Centre for the Great Barrier Reef World Heritage Area (CRC Reef) Effects of Line Fishing (ELF) experiment (Campbell et al., 2001; Mapstone et al., 2004). The ELF experiment, which began in 1995 and concluded in 2006, monitored line-caught fish populations from a group of six neighboring reefs in each of four regions extending over 7° of latitude along the GBR (Fig. 1; Mapstone et al.[6], 1996, 1997, 2004; Davies et al.[7]). At the start of the experi-

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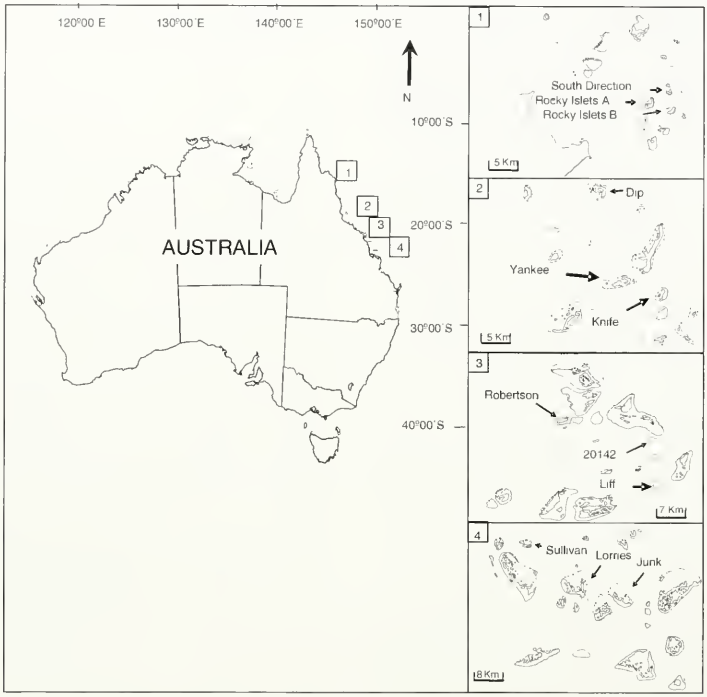

Figure 1

Great Barrier Reef, Australia. Study regions and reefs (1–4) from which common coral trout (*Plectropomus leopardus*) were collected are shown. 1 = Lizard Island; 2 = Townsville; 3 = Mackay; 4 = Storm Cay.

ment, four reefs in each region had been closed to fishing for 10–12 years under GBR Marine Park Zoning Plans (zoned Marine National Park B, MNP-B) and two reefs in each region had been open to fishing (zoned as General Use, GU). Two of the reefs closed to fishing remained closed during the experiment, other than to the annual research line fishing surveys. The other two closed reefs were each subjected to one year of fishing, in 1997 and 1999, after which they were closed again. The two reefs in each region that had historically been open to fishing were subjected to increased fishing pressure for one year (i.e., were temporarily opened). These reefs were then closed for five years before reverting to their original zoning status (GU).

All reefs were sampled each year in the austral spring (October–December) to coincide with the peak spawning period of the main target species, *P. leopardus*. Each reef was divided into six approximately equal-size, contiguous blocks, and sampled on a single day on each sampling occasion. Standardized commercial reef line fishing effort was distributed uniformly across two depth strata within each block. All fish caught were measured, tagged for later identification, and kept for weighing and for extraction of gonads and otoliths. For further sampling details of the ELF experiment see Davies et al.[7] and Mapstone et al. (2004). Samples of *P. leopardus* were aged by CRC Reef staff using standardized methods developed by Ferreira and Russ (1994).

Sample collection

Otolith morphological variables were analyzed from four-year-old *P. leopardus* collected in 1995 and 1999 from three reefs within each of the four regions (Fig. 1; Table 1). Four years is the youngest age at which *P. leopardus* in all regions are fully recruited to the fishing gear used in the ELF Experiment. Although the zoning status of a reef and the level of fishing pressure on it were unlikely to have affected otolith structure, one reef from each treatment regime in the ELF experiment was included from each region to avoid potential biases in spatial variation related to particular fishing histories. Thus, within each region, samples were analyzed from one MNP-B reef that was closed to fishing, one MNP-

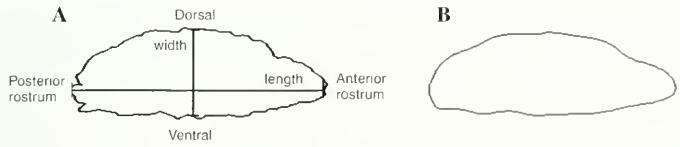

Figure 2

Example of a common coral trout (*Plectropomus leopardus*) otolith reconstructed by using (**A**) all of the 128 Fourier descriptors that were collected, and (**B**) the first and last 14 descriptors. Otolith orientation and measures of length and width are indicated.

Table 1

Study regions, reefs, and years for which the common coral trout (*Plectropomus leopardus*) was sampled over the Great Barrier Reef and examined for otolith morphology.

Region	Reef (GBRMPA number)	1995, 1999 replicates	Total length range (mm)
Lizard Island	Rocky Islet Reef A (14132a)	20, 6	304–495
	Rocky Islet Reef B (14132b)	20, 6	306–481
	South Direction Reef (14147)	20,12	350–468
Townsville	Knife Reef (18081)	8, 4	370–451
	Dip Reef (18039)	7,12	318–462
	Yankee Reef (18074)	20, 8	322–464
Mackay	unnamed reef (20142)	20, 18	322–456
	Liff Reef (20296)	20, 16	303–427
	Robertson Reefs (no2) (20136)	20, 11	342–514
Storm Cay	Junk reef (21131)	20, 15	345–422
	Lorries reef (21130)	20, 11	328–475
	Sullivan reef (21124)	18, 19	280–424
Total		213, 138	303–514

B reef that was open for one year of fishing and then closed, and one GU reef that was subjected to increased fishing for a year prior to closure for five years.

Because otoliths from only four-year-old fish were analyzed in 1995 and 1999, the two cohorts included individuals with nonoverlapping life histories. Consequently, individuals collected in 1995 were not exposed to the influence of the unusually large and persistent Cyclone Justin that influenced the southern half of the GBR throughout March in 1997, unlike those four-year-old fish collected in 1999. Standardizing sampling by age also minimized the potential for confounding spatial variation in otolith shape with ontogenetic changes.

Sagittal otoliths from up to 20 four-year-old *P. leopardus* were sampled from each reef each year (Table 1). Otoliths from fewer than 20 fish were analyzed only if less than this number were collected from a reef. This sampling design enabled the examination of broad (region) and fine (reef within region) spatial and temporal (1995 and 1999 cohorts) patterns in the otolith morphology of *P. leopardus* across much of the GBR, spanning an unusual environmental event (Cyclone Justin, 1997) that had the potential to significantly influence the results.

Morphological analysis

A microscope image (10× magnification) was projected onto a computer screen by using a video camera (Panasonic GP-KR222E, Panasonic, Matsushita Communication Industrial Co., Osaka, Japan. Whole otolith area, length, perimeter, and width (Fig. 2) and two shape indices (circularity and rectangularity) were recorded from each otolith by using the OPTIMAS image analysis system (OPTIMAS, vers. 6.51, Silver Spring, MD). Rectangularity was calculated as the area of the otolith divided by the area of its minimum enclosing rectangle, and circularity as the perimeter of the otolith squared divided by its area. The perimeter of the otolith was traced in a counter clockwise direction and digitized into 128 x-y equidistant coordinates by using the distal edge of the otolith rostrum as a common starting point

for the coordinates. A fast Fourier transform (FFT) was calculated as a Cartesian FFT. The Cartesian FFT uses the 128 *x-y* coordinates as complex numbers ($a + ib$), where a is the real component and ib the imaginary component, representing the amplitudes of the cosine and sine waves, respectively. The resultant 128 set of complex numbers or descriptors were subsequently normalized for differences in otolith position by setting the 0th descriptor to 0, and for size and rotation of the otolith by dividing all the descriptors with the first descriptor. The normalized descriptors ($a' + ib'$) were used to calculate the absolute value (harmonic) of each descriptor according to the following equation (Christopher and Waters, 1974):

$$Harmonic = \sqrt{a_n'^2 + (ib')_n^2}.$$

The harmonics were then used in combination with the other morphological variables and shape indices to compare otoliths between cohorts and among regions and reefs within regions.

The higher the number of equidistant points and subsequent complex numbers included in the model, the closer is the fit to the original shape. The main features of the otolith shape, however, are generally captured by the first 10–20 harmonics (e.g., Campana and Casselman, 1993; Friedland and Reddin, 1994). The minimum number of Fourier descriptors required to explain at least 90% of the recorded shape of the otoliths in our study was calculated similarly to the range-finding procedure of Smith et al. (2002). A total of 128 descriptors were collected from two randomly selected otoliths from each reef and cohort (24 in total) and normalized for position, size and rotation as described above. The shape of each otolith was reconstructed (by computing the inverse FFT) by using all the descriptors and then reconstructed by using only the first and last descriptors. The Euclidian distance between the inverse FFT using all the descriptors and the inverse FFT using only the first and last descriptors was defined as the maximum percent error of reconstruction, i.e. 100% reconstruction error (Smith et al., 2002). Because the Cartesian descriptors are asymmetrical around the middle frequency, both ends of the array are required in the reconstruction. Otolith shape was reconstructed, therefore, by using the first two and last two descriptors, the first three and last three descriptors, and so on until the first and last 22 descriptors were used. This range-finding test allowed us to estimate the decrease in mean percent reconstruction error by using more and more descriptors and it was estimated that 14 of the first and last descriptors were required for the reconstruction error to be less than 10%. See Figure 2 for a comparison of the otolith shape reconstructed from the first and last 14 descriptors and all 128 descriptors. These descriptors, therefore, were used in the statistical analyses to compare the spatial and temporal patterns in otolith shape of *P. leopardus*.

Statistical methods

The assumption of normality and homogeneity of variance for each morphological variable was examined by using Shapiro-Wilk's and Levene's tests, respectively, and homogeneity of the group covariance matrix by Box's *M* test. Variables of circularity, breadth and area were $\log_{10}$-transformed and Fourier harmonics 2, 4, 9, 11–14, 120–121, 114–118, and 123–127 square-root–transformed to conform to the assumption of normality and homogeneity of variances.

A relationship between otolith shape and otolith growth rate (assumed to be correlated to fish length) may confound spatial or temporal differences in otolith shape (Campana and Casselman, 1993). We minimized the potential for such effects by 1) including only fish with a fork length (FL) between 280 and 514 mm (overall FL for four-year-olds sampled during the ELF experiment in 1995 and 1999 ranged from 250 to 551 mm), and 2) standardizing morphological variables by fish FL where a significant relationship existed between the variable and FL before further analyses. The effect of FL on each morphological variable was examined by analysis of covariance (ANCOVA; Winer et al., 1991). Our primary interests in these analyses were 1) to test whether morphological variables differed with FL for any group of samples; and 2) if so, to test whether the slopes of regressions of morphological variable on FL were homogeneous among groups. If a significant regression was detected and homogeneous among groups, the effect of FL was removed from each measurement by using the relationship

$$O_{ij,adj} = O_{ij} + b.(FL_{ij} - MFL._j).$$

where $O_{ij,\,adj}$ = otolith morphological measurement of fish i adjusted to mean fork length of group j;
O_{ij} = original otolith morphological measurement for fish i from group j;
$b.$ = slope of the relationship O_{ij}:FL_{ij} common to **all** groups;
FL_{ij} = fork length of fish i in group j; and
$MFL._j$ = average fork length within group j.

If significant slopes of the relationship differed among groups, the correction for FL was made separately for each group by using the equation above, but by replacing the common slope ($b.$) with the group-specific slope (b_j). These corrections had the effect of scaling all morphological variables from all otoliths to their predicted group mean FL.

Multivariate analysis of variance (MANOVA; Tabachnick and Fidell, 1983) was used to investigate the effects of sex (females, males, and individuals in the process of changing sex; i.e., transitional fish) on otolith shape (MANOVA). A total of 302 of the 351 individuals had been examined for sex, of which 166 were females, 123 males and 13 transitional fish. Separate MANOVAs were computed for the one- and two-dimensional shape

variables and the Fourier harmonics by using a three-way crossed model (outlined below) with fixed factors: cohort, region, and sex. Data were pooled across reefs within regions owing to insufficient sample numbers to test for reef-specific effects.

A MANOVA was used to test for spatial and temporal differences in otolith shape. A principal component (PC; Tabachnick and Fidell, 1983) analysis was done first on the combined data set of both the shape variables and Fourier harmonics to reduce the number of variables to be incorporated in the MANOVA. The number of PCs to extract and subsequently include in the MANOVA was determined by examining the size of the eigenvalues (representing the variance explained by each PC), as well as their relative contribution to the percent variance explained compared to the other eigenvalues (i.e., scree test; Tabachnick and Fidell, 1983). The latter determines the number of PCs beyond which the addition of more PCs would contribute little to the variance explained by the solution (Tabachnick and Fidell, 1983). Wilk's lambda criterion was used to test for group differences in the MANOVAs. Sums of squares and degrees of freedom of interactions were pooled when the *F*-ratios of interaction effects were ≤1. Pooling increases the degrees of freedom for the denominator and consequently the power of the test of remaining (unpooled) effects in the analyses.

A posteriori univariate analysis of variance (ANOVA) was used to explore patterns for each of the PCs separately when significant effects were indicated in the MANOVA. The univariate linear model for the analysis of each PC was

$$x_{ijkl} = \mu + C_{i..} + R_{.j..} + r(R)_{.k(j)} + CR_{ij..} + Cr(R)_{ik(j).} + e_{l(ikj)},$$

where x_{ijkl} = the PC score for otolith l from cohort i, region j and reef k;

μ = the estimate of the population mean PC score over all cohorts, regions, reefs, and otoliths;

$C_{i...}$ = the fixed effect of cohort i averaged over regions and reefs;

$R_{.j..}$ = the fixed effect of region j averaged over cohorts and reefs;

$r(R)_{.k(j)}$ = the random variation attributable to reef k within region j averaged over cohorts; and

$e_{l(ikj)}$ = unexplained random variation associated with otolith l within cohort i, region j and reef k.

Tukey's honestly significant difference (HSD) test was used to determine which means differed following significant effects detected in the ANOVAs. The communalities (representing the proportion of the total variance of a variable accounted for by the PC) and variable loadings of the PCs that were significant in the ANOVAs were subsequently examined. A loading below 0.45 indicated that the variable explained less than 20% of the PC and therefore was not interpreted further.

Finally, two forward stepwise canonical discriminant analyses (CDAs; Tabachnick and Fidell, 1983) were computed by using the shape variables and Fourier harmonics to examine the otolith shape of *P. leopardus* in multivariate space and to investigate whether otolith shape could be used to classify samples to spatial scale and cohort of origin. The factor used as a separating variable in the CDA depended on the significant effects determined in the MANOVA (i.e., cohort, region, or reef [region], or any interactions between these factors). The CDA was used in this way as a confirmatory technique. Wilk's lambda criterion was used to test for significant differences between the discriminant functions. Jackknife classification was used to minimize potential bias in the reclassification of individuals.

Results

Slopes of the relationship between FL and several otolith morphological variables for *P. leopardus* differed among a range of spatial scales and between cohorts (Table 2). The within-group slope, therefore, was calculated for each group according to the level at which the slopes of the relationship differed and was used to correct for the influence of FL (Table 2). For some variables, the common between-group slope was used to correct for the influence of FL because there was a significant overall relationship between the variable and FL, which was homogeneous among groups (ANCOVA homogeneity of slopes test, $P>0.05$; Table 2). No morphological variable was significantly correlated with FL after standardization. Furthermore, shape variables and Fourier harmonics were not significantly different between otoliths of females, males or transitional fish (MANOVA, $P>0.05$). The morphological data, therefore, were pooled across sex for the remainder of the analyses.

Principal component analysis (PCA)

Four PCs were extracted from the analysis of the combined data set of shape variables and Fourier harmonics and included in the MANOVA (Table 3). The communalities ranged between 0.11 and 0.88, and some morphological variables were better defined by the PC solution than others (Table 3). About 44% of the total variance in the morphological data was explained by the four extracted PCs (17.9%, 10.2%, 9.9% and 5.9% by PC I, II, III, IV, respectively). A combination of higher order harmonics describing the finer details of the otolith outline, and lower order harmonics, perimeter, length, and circularity representing the broad shape of otoliths explained most of the variation in PC I and III (Table 3). Variation in the broader details of otolith shape also accounted for most of the variation in PC II and PC IV; otolith area, breadth, perimeter, length, and harmonic eight explained most of the variation in PC II and breadth and harmonic 127 explained most of the variation in PC IV (Table 3).

Table 2

Results of the homogeneity of slopes test for the influence of fish fork length (FL) on otolith morphological variables of four-year-old *Plectropomus leopardus*. The level of correction represents the level at which the slopes were heterogenous. For example, the level of correction "reef(region)" means that the slopes of the relationship between FL and a morphological variable differed among reefs nested within regions and that the slope for each reef was used to correct for the influence of FL. Level of correction "FL" means that there was a significant overall relationship between FL and a morphological variable, but that the slopes of this relationship were homogenous among reefs(region), regions and cohorts. Only variables with a statistically significant relationship with FL are shown.

Variable	df	F	P	Level of correction
Log_{10} breadth	8, 306	1.99	0.0467	reef(region)
Log_{10} circularity	8, 306	1.99	0.0479	reef(region)
Length	3, 315	4.05	0.0075	region
Log_{10} area	8, 306	2.01	0.0452	reef(region)
Perimeter	8, 306	2.34	0.0187	reef(region)
Rectangularity	1, 341	14.43	0.0002	FL
Sqrt harmonic 2	1, 349	11.15	0.0009	FL
Harmonic 3	1, 349	10.32	0.0014	FL
Sqrt harmonic 4	1, 349	6.90	0.0090	FL
Harmonic 5	3, 314	3.44	0.0171	cohort × region
Harmonic 6	7, 314	2.12	0.0410	reef(region)
Harmonic 7	1, 349	13.56	0.0003	FL
Sqrt harmonic 9	7, 307	2.30	0.0270	cohort × reef(region)
Sqrt harmonic 13	1, 349	8.05	0.0048	FL
Sqrt harmonic 14	7, 317	3.31	0.0021	reef(region)
Sqrt harmonic 114	1, 327	8.69	0.0034	vohort
Sqrt harmonic 115	7, 307	2.48	0.0170	cohort × reef(region)
Sqrt harmonic 116	7, 317	3.95	0.0004	reef(region)
Sqrt harmonic 117	7, 317	2.89	0.0061	reef(region)
Sqrt harmonic 118	3, 314	2.90	0.0354	cohort × region
Harmonic 119	1, 349	6.79	0.0096	FL
Sqrt harmonic 120	3, 325	2.91	0.0346	region
Sqrt harmonic 121	7, 307	2.10	0.0435	cohort × reef(region)
Harmonic 124	3, 314	4.01	0.0080	cohort × region
Harmonic 125	1, 349	10.79	0.0011	FL
Harmonic 126	1, 349	31.76	<0.0001	FL
Harmonic 127	1, 327	4.37	0.0373	cohort

The MANOVA of the four PCs identified significant differences in the PC scores of otolith shape among regions, but were not consistent between cohorts (1995 and 1999; cohort×region interaction, Table 4). Univariate ANOVAs indicated that these differences were due to variation in PC II among regions and in PC IV among reefs within regions—both spatial patterns varying depending on the cohort in consideration (Table 5). Differences in PC II were due to differences between Lizard Island and Mackay regions in 1995 and between cohorts in Mackay (Fig. 3A; HSD, $P<0.05$). The apparent inconsistency between the significant reef within region effect in the ANOVA (PC IV) and no such reef effect detected in the MANOVA is most likely explained by the difference between two reefs in the Lizard Island region, for which there was a significantly lower mean PC IV score for Reef 14132a than for Reef 14147 in 1995, whereas the reverse was observed in 1999 (Fig. 3B; HSD, $P<0.05$). There was also a significant difference among cohorts on Reef 14132a (Lizard Island) and Reef 20296 (Mackay Region; Fig. 3B; HSD, $P<0.05$).

Although only explaining 18% (PC II and PC IV combined) of the variation in our morphological data, the PC analysis indicated that the presence of at least two stocks of *P. leopardus* on the GBR in 1995, one in the northern part of the GBR (Lizard Island) and one in the southern part (Mackay), whereas one homogeneous stock was indicated in 1999.

Table 3

Variable communalities and loadings on the four significant principal components (PCs) explaining 44% of the total variance in the otolith morphological data of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef.

		Loadings			
Variable	Communalities	PC I	PC II	PC III	PC IV
Perimeter	0.88	0.39	0.69	0.51	0.01
Length	0.85	0.07	0.57	0.71	0.14
Log_{10} area	0.81	−0.05	0.80	0.32	−0.27
Log_{10} breadth	0.80	−0.03	0.70	−0.10	−0.55
Harmonic 127	0.78	0.18	−0.16	0.65	0.55
Log_{10} circularity	0.76	0.67	0.13	0.42	0.33
Sqrt harmonic 4	0.70	0.80	0.04	−0.21	−0.09
Harmonic 6	0.64	0.72	0.18	−0.27	−0.11
Harmonic 5	0.58	0.63	−0.29	0.27	−0.15
Harmonic 8	0.51	0.17	0.57	−0.38	0.09
Harmonic 10	0.49	−0.32	0.44	−0.29	0.34
Sqrt harmonic 2	0.49	0.70	0.00	−0.04	0.03
Harmonic 3	0.49	−0.40	−0.05	0.57	0.01
Harmonic 122	0.45	0.43	0.40	−0.25	0.21
Sqrt harmonic 13	0.44	0.58	−0.08	−0.07	−0.30
Sqrt harmonic 117	0.41	0.42	−0.21	0.11	−0.42
Harmonic 7	0.41	0.54	−0.23	0.06	0.25
Sqrt harmonic 120	0.40	0.37	0.26	−0.32	0.30
Sqrt harmonic 11	0.37	0.54	−0.12	0.03	−0.25
Harmonic 119	0.37	0.45	−0.30	0.22	−0.14
Harmonic 125	0.35	−0.22	0.02	0.55	0.03
Sqrt harmonic 115	0.35	0.33	−0.12	0.22	−0.42
Sqrt harmonic 121	0.31	0.39	−0.37	0.16	−0.01
Harmonic 124	0.30	0.48	0.11	0.03	0.24
Sqrt harmonic 116	0.26	0.30	0.14	−0.35	0.18
Sqrt harmonic 118	0.26	0.49	0.02	−0.11	0.06
Sqrt harmonic 114	0.18	0.19	0.00	−0.37	0.10
Sqrt harmonic 12	0.18	0.22	−0.11	0.33	−0.05
Harmonic 126	0.16	0.32	0.18	0.04	0.13
Sqrt harmonic 9	0.14	0.09	−0.20	−0.05	0.30
Sqrt harmonic 123	0.14	0.27	−0.03	−0.17	0.18
Rectangularity	0.13	−0.25	−0.17	−0.18	0.08
Sqrt harmonic 14	0.11	0.30	−0.09	−0.02	0.10

Discriminant analyses

Two stepwise canonical discriminant analyses (CDAs) were computed for the morphological variables (Fourier harmonics and shape variables combined) in response to the significant cohort × cegion effect in the MANOVA of the PC scores. First, separate CDAs were done for each region using cohort as the separating variable and second, separate CDAs were done for each cohort by using region as the separating variable. The region-specific CDA, where cohort was used as a separating variable, showed a significant first discriminant function (DF) for all four regions, accounting for 100% of the variance in the data (Table 6). Some separation was observed in the distribution of the DF I scores between the two cohorts within each region, although the temporal pattern was not consistent across regions (Fig. 4). Likewise, the cohort specific CDA using region as a separating variable showed some separation between the four regions in the first two significant DFs of cohort 1995 (explaining 59.9% and 30.7% of the variance, respectively) and one significant function of cohort 1999 (explaining 100% of the variance, Table 6). The means of the DF I scores in the Lizard Island and

Townsville regions were distinctly greater than those of the Mackay and Storm Cay regions in 1995 (HSD, $P<0.05$; Fig. 5A) and in Townsville were greater than the Mackay and Storm Cay regions in 1999 (HSD, $P<0.05$; Fig. 5B).

Different combinations of harmonics 9, 114, 118 describing the finer details of the otolith shape, and harmonic 124 and shape variables area and circularity representing the broad details of otolith shape, were selected into the DFs to maximize the separation of cohorts within regions (Table 7). The primary predictor variables selected for separating regions in each of the cohorts were similar to those selected in the region-specific CDA, although the variables were not the same in each cohort (Table 7). Between 66.7% and 76.3% of *P. leopardus* within a region could be correctly classified to their cohort of origin (Table 8). Fewer cohort specific individuals could be classified to a region however;

Table 4

Results of MANOVA comparing principle component (PC) I–IV scores of otolith shape from two cohorts of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef. *P*-values in bold indicate significant differences ($P<0.05$).

Factor	Wilks' lambda	*F*	df	*P*
Cohort	0.3800	2.04	4, 5	0.2269
Region	0.0513	2.34	12, 14	0.0687
Cohort×region	**0.0315**	**3.04**	**12, 14**	**0.0269**
Reef(region)	0.8880	1.19	32, 1167	0.2126
Cohort×reef(region)	0.8900	1.18	32, 1167	0.2318

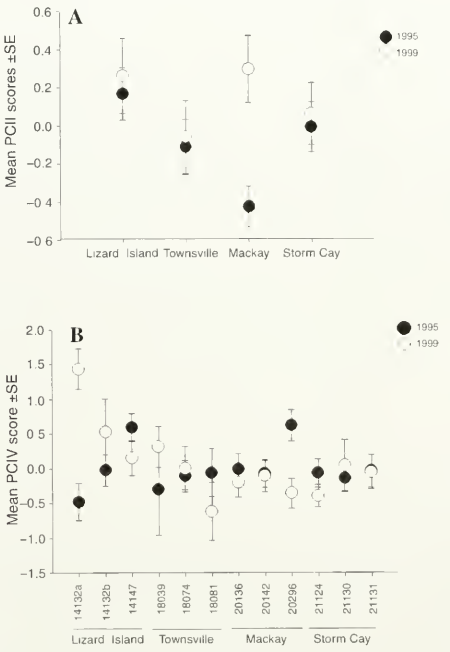

Figure 3

Mean (**A**) principal component (PC) II scores per region and cohort, and (**B**) PC IV scores per reef within region and cohort of four-year-old common coral trout (*Plectropomus leopardus*), collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef.

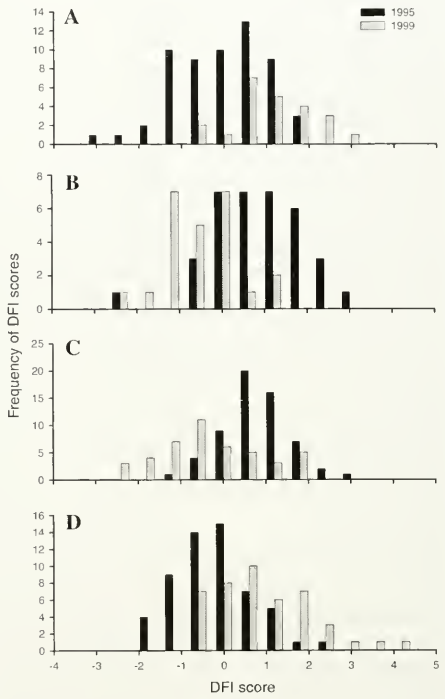

Figure 4

Frequencies of discriminant function (DF) I scores from otolith morphological variables (Fourier harmonics and shape variables combined) per cohort (sampled in 1995 and 1999) for regions (**A**) Lizard Island, (**B**) Townsville, (**C**) Mackay, and (**D**) Storm Cay for four-year-old common coral trout (*Plectropomus leopardus*), from the Great Barrier Reef. (The data were pooled across reefs within regions.)

34.3% and 39.7% were correctly classified for cohorts sampled in 1995 and 1999, respectively (Table 9).

Discussion

Spatial and temporal variation in otolith structure

This study detected differences in the otolith shape of *P. leopardus* at different spatial and temporal scales across the Great Barrier Reef (GBR), Australia. Although the spatial patterns in otolith shape of *P. leopardus* were not always consistent among different types of shape variables, two main inferences can be made from our results. Firstly, our results indicate that otolith morphology can be useful for identifying groups of individuals of this species that are likely to have spent a significant part of their lives in different environments and therefore may indicate potential stock separation. Overall otolith shape suggested the presence of at least one southern and one northern stock along the GBR. The Storm Cay and Mackay regions consistently belonged to the southern stock and the Lizard Island region to the northern stock, and it was inconclusive as to which stock individuals in the Townsville region belonged. It is possible that the main morphological features of otoliths are established in the larval stage and that large amounts of larval dispersal and mixing between areas results in overlap of signatures between stocks. Finer details of otolith shape, however, are most likely influenced by environmental processes during the post larval phase and may therefore provide insights to the separation of stocks during postlarval life.

Although otolith shape also suggested variation at a smaller, among reef, spatial scale (hundreds to thousands of m) the significant differences in the multivariate morphological measurement (PC IV) occurred only between two reefs in the Lizard Island region, and therefore it seems unlikely that such small-scale separation is a common phenomenon on the GBR. Nevertheless, the presence of some difference among reefs emphasizes the importance of careful and sufficient sampling in order to capture the range of values manifest in small-scale, presumably random, variation within regions and to avoid erroneously ascribing to regional structure what are really a reflection of local-scale variation. Given the hydrodynamic mixing over scales of kilometers, we consider it unlikely that reef-scale variations in morphological variables represent persistent environmentally induced patterns in stock structure.

Table 5

Results of ANOVAs comparing otolith principle component (PC) scores of otolith structure from two cohorts of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef. Only final analyses resulting from pooled terms with $F \leq 1$ are shown. P-values in bold indicate significant differences ($P<0.05$). Only PCs with significant differences are shown. MS=mean square.

Variable	Factor	df	MS	F	P
PC II	Cohort	1	1.5165	1.60	0.2067
	Region	3	0.8057	0.47	0.7126
	Reef(region)	8	1.7209	1.82	0.0732
	Cohort×region	**3**	**3.0900**	**3.26**	**0.0217**
PC IV					
	Cohort	1	0.3246	0.11	0.7473
	Region	**3**	**3.2901**	**8.11**	**0.0083**
	Cohort×region	3	3.5574	1.21	0.3675
	Reef(region)	8	0.4059	0.43	0.9011
	Cohort×reef(region)	**8**	**2.9452**	**3.14**	**0.0020**

Table 6

Significance test of cohort-specific and region-specific canonical discriminant analysis (CDA) of shape variables and Fourier harmonics combined from otoliths of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in two cohorts, 1995 and 1999 on the Great Barrier Reef. Only significant discriminant functions (DF) are shown. DF=discriminant function; df=degrees of freedom.

Scale	Factor	DF	Wilks' lambda	χ^2	df	P
Spatial scale						
Lizard Island	Cohort	I	0.7818	19.21	2	<0.0001
Townsville	Cohort	I	0.6863	20.89	3	0.0001
Mackay	Cohort	I	0.7685	26.34	4	<0.0001
Storm Cay	Cohort	I	0.7683	25.43	3	<0.0001
Temporal scale						
1995	Region	I to III	0.7573	56.72	12	<0.0001
1995	Region	II to III	0.8918	23.36	6	0.0006
1999	Region	I	0.91	11.95	3	0.0075

The second inference from our results is that regional patterns in otolith shape are not always consistent among cohorts and may be subject to temporally dynamic events such as large-scale environmental perturbations. Ignoring such temporal signals could give misleading information about stock structure. A single homogenous stock of *P. leopardus* may have been suggested if otolith structure based on the 1999 PCA results alone were considered, whereas two potential stocks would be inferred from both the PCA and CDA analyses of the 1995 data (Figs. 2A; 5A). In addition, cohorts were distinguishable within all regions based on the frequency distributions of DF scores. Other investigations of the interannual stability in otolith morphology of marine fishes have found differences between years, as well as age groups (Castonguay et al., 1991; Campana and Casselman, 1993; Begg and Brown, 2000; Begg et al., 2001). Consequently, when using otolith morphology to investigate stock structure, it is preferable to compare multiple cohorts with individuals of the same age, collected over several years. Such a sampling design would minimize confounding spatial variation in otolith shape with particular times of sampling and derive a time-averaged assessment of the spatial structure of a stock.

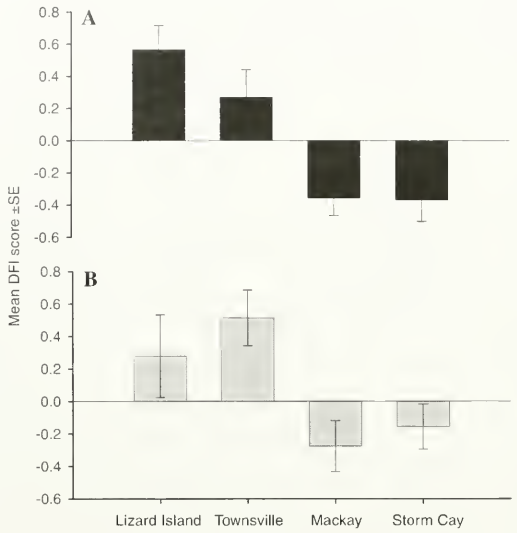

Figure 5

Mean ±SE of discriminant function (DF) 1 scores from otolith morphological variables (Fourier harmonics and shape variables combined) per region for (A) cohort 1995, and (B) cohort 1999 in four-year-old common coral trout (*Plectropomus leopardus*) from the Great Barrier Reef. (The data were pooled across reefs within regions.)

The spatial and temporal patterns in otolith shape are in part consistent with the assessment (based on otolith microchemistry) of stock structure of *P. leopardus* on the Great Barrier Reef (Bergenius et al., 2005). Differences in otolith chemistry of *P. leopardus* collected at the same spatial and temporal scales as those considered in this study have indicated the presence of two or three regional stocks. Thus, although the number and potential boundaries of phenotypic stocks based on otolith chemistry and otolith structure remain uncertain, the combined results of these studies emphasize the potential presence of several stocks of *P. leopardus* on the GBR and indicate a north-south demarcation. Differences in both otolith

Table 7

Canonical coefficient function representing correlation between the morphological variables (Fourier harmonics and shape variables combined) and significant discriminant functions (DFs), separating two cohorts (1995 and 1999) of four-year-old *Plectropomus leopardus* within each of four regions of the Great Barrier Reef. All variables selected in the models are shown, but variables with loadings <0.45 are not interpreted further.

Variable	Lizard Island DF I	Townsville DF I	Mackay DF I	Storm Cay DF I	1995 DF I	1995 DF II	1999 DF I
Log_{10} area			−0.62		0.59	−0.37	
Rectangularity				0.38			
Log_{10} circularity		−0.58					1
Sqrt harmonic 9		0.49	0.57				
Sqrt harmonic 114				0.62			
Sqrt harmonic 115	−0.24						
Sqrt harmonic 118	0.84				−0.46	0.23	
Sqrt harmonic 123			0.35				
Sqrt harmonic 124		0.22		0.49	0.45	0.52	
Sqrt harmonic 125			0.41		−0.12	0.69	

Table 8

Correctly classified individuals of four-year-old *Plectropomus leopardus* per cohort (1995 and 1999) in each of four regions of the Great Barrier Reef.

Cohort	Lizard Island	Townsville	Mackay	Storm Cay
1995	63.79	71.43	78.33	76.79
1999	73.91	83.33	70.45	63.64
Total	66.70	76.30	75.00	71.00

Table 9

Correctly classified individuals of four year old *Plectropomus leopardus* per region on the GBR in each of two cohorts (1995 and 1999).

Region	1995	1999
Lizard Island	39.66	17.39
Townsville	28.57	58.33
Mackay	45.00	53.49
Storm Cay	41.07	11.36
Total	39.70	34.30

shape and chemistry indicated that the movements of adults of *P. leopardus* may be limited and are consistent with the presumed sedentary (reef-specific) habit of most serranids after settlement (e.g., Chapman and Kramer, 2000; Stewart and Jones, 2001). Our results confirm those of several tagging studies of *P. leopardus* on the GBR which showed that individuals are unlikely to move among reefs after settlement (Davies, 1995; Zeller, 1998; Zeller and Russ, 1998). Such limited inter-stock movement of adults means that the recovery rate of stocks after significant harvest is largely (if not solely) dependent on some unknown level of larval dispersal. Further investigations, therefore, are required to clarify the implications of this potential stock structure of *P. leopardus* to ensure sustainable harvests at the appropriate scale for both management and the stock structure of the fish.

Reasons for temporal and spatial variation in otolith structure

Little is known about what processes influence the expression of traits responsible for otolith shape (Ihssen et al., 1981). Differences in growth rate has been the main reason given for differences in linear morphological variables of otoliths (e.g., Reznick et al., 1989; Secor and Dean, 1989; Begg et al., 2001), as well as outline shape variables (e.g., Castonguay et al., 1991; Smith, 1992; Campana and Casselman, 1993; Begg and Brown, 2000). In our study, *P. leopardus* subsamples were restricted to a certain size range to minimize the potential of a growth rate effect that could confound spatial or cohort related differences in otolith shape. Significant differences in growth rates (indicated by mean FL of four-year-olds), however, were apparent among reefs within regions in the complete sample from the ELF experiment (Bergenius et al.[8]), whereas there was no consistency in the patterns of variation in FL and any of the otolith morphological variables. It is possible that the large variation in FL among reefs could have masked potential differences in broad-scale regional differences in growth rates, or that some other developmental rate, such as maturation or reproductive output, were more important in influencing the otolith shape of *P. leopardus*.

Spatial and temporal variability in otolith shape would be expected in *P. leopardus* populations along the GBR given the natural variability in biological and hydrodynamic factors between reefs and regions (Wolanski, 1994), which in turn could affect various fish developmental rates. There was no monotonic latitudinal trend apparent in any of the otolith morphological variables related to a temperature gradient. The maximum difference in monthly average sea surface temperature among the latitudes examined in our study is typically less than 2°C (Lough, 1994). In contrast, there is regional (broad spatial scale) variability in the upwelling and inflow of cool nutrient rich oceanic water across the continental shelf of the GBR (e.g., Andrews and Gentien, 1982; Andrews, 1983; Wolanski, 1994; Middleton et al., 1995) which could potentially influence fish developmental rates through changes in food availability or "step-wise" patterns in water temperature.

There is also a possibility that the temporal variability in otolith shape of *P. leopardus* collected before and after Cyclone Justin in 1997 was related to associated temperature or other climatic changes. Cyclone Justin was an unusually large cyclone that remained in the Coral Sea adjacent to the GBR for over three weeks during March 1997. It caused a large and rapid drop in water temperature over the southern half of the GBR (south of ~17–18°S) during this time, and bottom water temperatures dropped in just one month (March) to below the average winter minimum not usually reached until July (AIMS[5]). Our study revealed a significant difference in otolith shape between nonoverlapping cohorts sampled in 1995 and 1999 in the Mackay region, which is one of the regions where the temperature changes would have been greatest.

Management and future directions

Although differences in otolith shape of *P. leopardus* may give an indication of stock structure, an examination of the relevance of these patterns for fisheries management should be the next step. A recent increase in the total

[8] Bergenius M. A. J., B. D. Mapstone, G. R. Russ, and G. A. Begg. 2005. Unpubl. data from the Effects of line fishing experiment (Mapstone et al., 2004). CRC Reef Research Centre, Townsville, Australia. [Data are on files at the CRC Reef Research Centre, James Cook University, Townsville, Queensland 4810, Australia.]

area of the GBR Marine Park (designated as marine national park zones [or no-take zones]) from about 5% to 33% enhances the potential for displacement of fishing effort between regions. If the proposed stocks have different life history characteristics and, potentially, different fishery productivities, less productive stocks may be subjected to greater harvest levels and increased risk of local depletion. Information on vital life history characteristics (e.g., growth, mortality, and maturity) is therefore needed to examine the potential impacts of fishing and related harvest strategies for the postulated stocks. Moreover, until more is known about how larvae relate between stocks, prudent and precautionary management should recognize groups of fish that function as individual units or stocks in response to harvest and management (Haddon and Willis, 1995).

Otoliths are often collected during routine sampling undertaken as part of the monitoring procedures and assessments of exploited fish stocks. As a result there may be large archives of otoliths available for morphological analyses in most fisheries laboratories. We therefore suggest that patterns in otolith morphology provide a cost and time effective starting point for directing further research on groups of harvested coral reef fishes that have lived at least parts of their life in different environments.

Acknowledgments

Funding for this work was provided by the Australian Cooperative Research Centres Program through the Cooperative Research Centre for the Great Barrier Reef World Heritage Area, and the Fisheries Research and Development Corporation, Great Barrier Reef Marine Park Authority and James Cook University. We thank the numerous members of the CRC Reef Effects of Line Fishing Team for the collection and processing of samples, especially Dong Chung Lou, Ashley Williams, and Gary Russ for aging *Plectropomus leopardus*. Simon Robertson provided guidance with the Fourier analysis.

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Abstract—The western butterfish (*Pentapodus vitta*) is numerous in the bycatch of prawn trawling and recreational fishing in Shark Bay, Western Australia. We have thus determined crucial aspects of its biological characteristics and the potential impact of fishing on its abundance within this large subtropical marine embayment. Although both sexes attained a maximum age of 8 years, males grow more rapidly and to a larger size. Maturity is attained at the end of the first year of life and spawning occurs between October and January. The use of a Bayesian approach to combine independent estimates for total mortality, Z, and natural mortality, M, yielded slightly higher point estimates for Z than M. This result indicates that *P. vitta* is lightly impacted by fishing. It is relevant that, potentially, the individuals can spawn twice before recruitment into the fishery and that 73% of recreationally caught individuals are returned live to the water.

Biological characteristics and mortality of western butterfish (*Pentapodus vitta*), an abundant bycatch species of prawn trawling and recreational fishing in a large subtropical embayment

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Manuscript submitted 14 October 2005 to the Scientific Editor's Office.
Manuscript approved for publication 14 November 2005 by the Scientific Editor.
Fish. Bull. 104:512–520 (2006).

The family Nemipteridae (threadfin breams) is found in tropical and subtropical waters of the Indo-west Pacific (Nelson, 1994). The western butterfish (*Pentapodus vitta*) (also known as "striped whiptail"[1]) is a small benthic nemipterid, which is endemic to Western Australia (Russell, 1990) and very numerous in Shark Bay on the west coast of this state (Heithaus, 2004). It is also very abundant in the bycatch of the prawn trawl and recreational fisheries in this large subtropical environment. However, as with the vast majority of bycatch species in embayments, no estimate has been made of the mortality of *P. vitta* due to fishing. Furthermore, although *P. vitta* is very abundant in certain environments, there are no data on the age composition, growth, and reproductive biology based on validated age data for a population of this species. Indeed, previous studies of the Nemipteridae have focused almost entirely on species of *Nemipteris* and *Scolopsis*, which are widely distributed throughout the Indo-Pacific, where they are an important component of commercial and artisinal fisheries (Sainsbury and Whitelaw, 1984; Young and Martin, 1985; Murty et al., 1992; Zacharia, 1998).

The present study elucidates key aspects of the biology of *P. vitta* and, in particular, length-weight relationships, size and age compositions, growth, size and age at maturity, duration of the spawning period, and mortality. Focus is also placed on ascertaining whether this species is hermaphroditic, as is the case with certain other nemipterids (Young and Martin, 1985). The question of whether the mortality of a species with the "characteristics" of *P. vitta* is particularly attributable to sub-

[1] FishBase. http://www.fishbase.org/search.php [accessed June 2006].

stantial trawling and recreational fishing in an embayment has also been explored. For this purpose, we have used a model that reconciles the often imprecise and conflicting estimates of total and natural mortality that are obtained by using traditional approaches (Hall et al., 2004).

Materials and methods

Sampling regime

766 *P. vitta*, ranging from 90 to 198 mm in fork length (FL), were collected by trawling throughout Shark Bay in November and December 1997. Trawling was conducted at night by using twin 11-m prawn trawl nets with 50-mm mesh in the panels and 44-mm mesh in the codends, as are employed by commercial prawn trawl operators in Shark Bay. Each trawl lasted 20 minutes. The samples collected were used for estimating the mortality of western butterfish in Shark Bay. *Pentapodus vitta* (n=339), ranging from 31 to 215 mm in fork length, were also collected in many months from 1999 to 2004 by using trawls, hook-and-line fishing, and beach seines. These samples were used to obtain aging, growth, and reproductive data in the study.

Relationships of total length and weight to fork length

The fork length (FL) of each fish, and the total length (TL) of each fish whose caudal fin was not damaged, were measured to the nearest 1 mm. The relationship between TL and FL of each sex was then calculated by using the equation

$$TL = a + b \times FL,$$

to enable the TL of any fish with a damaged caudal fin to be estimated from its FL. The weight of each fish (W) was recorded to the nearest 1 g. The relationships between the fork length and weight of females and males were described by the equation

$$\log W = \log a + b \log FL.$$

Analysis of covariance (ANCOVA, α=0.05) was used to determine whether the relationships between TL and FL and between weight and FL of the males and females of *P. vitta* were significantly different (Zar, 1999).

Validation of the aging method and age determination

The sagittal otoliths of each *P. vitta* were removed, cleaned, and stored in labelled paper envelopes. Because a preliminary examination demonstrated that the growth zones were often easier to discern in sectioned than in whole otoliths, all fish were aged by using sectioned otoliths. Transverse sections of each otolith, 0.3–0.5 mm thick, were cut through the primordium by using a low-speed jewellery saw and then ground using 9-μm lapping film. These sections were then mounted on glass slides and viewed with transmitted light under a dissecting microscope.

Validation that a single growth zone is formed each year in otoliths of *P. vitta* was undertaken by using marginal increment analysis. The distance between the outer edge of the outermost opaque zone and the periphery of the otolith section (the marginal increment) was measured on the sectioned otoliths of each fish caught between June 1999 and May 2000. The marginal increment was then expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. All measurements were made with the Leica Image Manager 1000 (Leica Microsystems AG, Wetzlar, Germany).

Ages were assigned to each *P. vitta* on the basis of the number of opaque zones (annuli) in sectioned otoliths and by taking into account the dates of capture and the birth date of the fish. The birth date was designated as 1 December because this date corresponded approximately to the mid-point of the period when, on the basis of gonadosomatic indices and the trends shown by gonadal and oocyte development, *P. vitta* spawn (see "Discussion" section). The opaque zones were counted in the region between the primordium and the proximal surface along the ventral and dorsal margins of the sulcus acousticus, where the opaque bands were usually well defined and thus easily identified. The opaque zones in each otolith were counted without knowledge of the length or date of capture of the fish from which that otolith had come.

The precision of the counts from 175 *P. vitta* otolith sections made by the senior author (JCM) on two separate occasions and between JCM's second count and a count made by another experienced reader, was assessed by using the index average percent error (IAPE) of Beamish and Fournier (1981). The IAPE values were low (i.e., 0.7%) for the two counts made by the senior author (JCM)) and for JCM's second count and that of the independent reader (i.e., 3.9%), demonstrating a high level of precision for the otolith readings. Because the senior author was more experienced in reading the otoliths of *P. vitta*, his second round of counts (and these were almost invariably the same as in the first round of counts) was used for determining the ages of individual fish.

Growth

Fish caught by all methods in all months (except those obtained during extensive trawling in November and December 1997)—fish that collectively covered the full size range of *P. vitta*, were used to provide data for constructing growth curves. The large samples collected by trawling in November and December 1997 were excluded because they would have introduced an excessive bias towards the larger fish at younger ages (see Ricker

[1975] for importance of limiting bias by using data from multiple sampling methods). Von Bertalanffy growth equations were fitted to the fork lengths of the female and male fish at their estimated ages at capture by using nonlinear regression in the Statistical Package for the Social Sciences software (SPSS 12.0.2 for Windows, SPSS Inc., Chicago, IL). The lengths at age of small fish whose sex could not be determined were allocated randomly to both the male and female data sets used for calculating the growth curves. The von Bertalanffy growth equation is

$$L_t = L_\infty(1 - \exp^{-k(t-t_0)}),$$

where L_t = the estimated length at age t;
L_∞ = the asymptotic length;
k = the rate at which L_t approaches L_∞; and
t_0 = the hypothetical age at zero length.

A likelihood-ratio test was used to compare the growth curves of the females and males of *P. vitta* (Cerrato, 1990). The hypothesis that a common growth curve could be fitted for the two sexes was rejected at the $\alpha = 0.05$ level of significance if the test statistic, calculated as twice the difference between the log-likelihoods obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters (i.e., 3) in the two approaches.

Reproductive biology

The gonads of each fish that could be sexed macroscopically were removed and weighed to the nearest 0.01 g and, in the case of ovaries, staged macroscopically by using the scheme of Laevastu (1965) and the histological characteristics of the ovaries. For histology, ovaries of a random subsample of female *P. vitta* from each month of the year were preserved in Bouin's fixative for 48 hours, after which they were dehydrated in an ascending series of alcohol concentrations, embedded in paraffin wax, cut into 6-μm thick sections, and stained with either Ehrlich's haematoxylin and eosin or Mallory's trichrome (Humanson, 1972). On each histological slide, the maximum and minimum diameters of 30 randomly selected oocytes, which had been sectioned through their nuclei, were recorded to the nearest 5 μm. The mean of these two measurements for each oocyte was considered to represent the diameter of that oocyte (see Foucher and Beamish, 1980).

The gonadosomatic indices (GSIs) of females and males ≥1 year of age were determined from the equation

$$W1/W2 \times 100,$$

where $W1$ = weight of gonad; and
$W2$ = weight of whole fish minus the weight of gonad.

Mortality

Age-frequency distributions for female and male *P. vitta* caught during extensive trawling in November and December 1997 were used to estimate the instantaneous rate of total mortality (Z) for both females and males. Age classes on the descending limb of the age-frequency distribution for each sex (i.e., immediately after the peak in this distribution), were considered fully recruited to the fishery (Ricker, 1975). The catch curve for each sex was analysed by using the assumptions that Z and the levels of annual recruitment are constant and that the age composition of fully recruited fish represents a random sample from a multinominal distribution with uniform selectivity from the age of full recruitment (Hall et al., 2004). The value of Z was estimated by maximizing the log-likelihood by using the SOLVER routine in Microsoft™ Excel (vers. 2002, Microsoft Inc., Redmond, WA). The data for *P. vitta* were randomly resampled with replacement and analyzed to create 1000 sets of bootstrap estimates. The point estimate for Z was taken as the median of the 1000 bootstrap estimates. The 95% confidence limits were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values. The likelihood-ratio test used to compare growth curves was also used to compare the catch curves for the two sexes.

Estimates of natural mortality, M, for female and male *P. vitta* were calculated from the relationship between natural mortality, growth, and water temperature (Pauly, 1980). This relationship was refitted to Pauly's data for 175 fish stocks by using SPSS 12.0.2 for Windows (SPSS Inc., Chicago, IL). The values of k (per year) and L_∞ (cm TL), estimated from the asymptotic FL in the growth curves derived for *P. vitta*, and the water temperature, T, were then inserted into SPSS to obtain point estimates and associated 95% confidence limits for M, thereby taking into account the uncertainty of the parameter estimates and the variation of the data around the regression line. The mean annual bottom water temperature in Shark Bay is 23.1°C (data provided by Department of Fisheries Western Australia).

The values for mortality, derived for each sex by using the above approaches, were combined with the estimates of total mortality obtained from the maximum recorded ages of the two sexes with Hoenig's (1983) regression model for fish and those obtained with a simulation approach (Hall et al., 2004). This method reconciles the inconsistencies among the individual estimates of mortality and, through combining the different values, improves the precision of the resulting estimates of natural and total mortality. To provide a more precise estimate, the simulation routine was modified slightly from that described by Hall et al. (2004) to use the number of males or females within the sample that were older than a specified age rather than the age associated with the oldest of those fish.

Results

Relationships of total length and weight to fork length

The relationships between the FL and TL of females and males, which covered essentially the full size range of *P. vitta*, did not differ significantly ($P>0.05$) and therefore the length data for the two sexes were pooled. The linear relationship between FL and TL for both sexes of *P. vitta* combined is described by the equation

$$TL = -2.35 + 1.12\ FL \qquad (n=344,\ r^2=0.99).$$

Moreover, because the relationship between weight and fork length of western butterfish did not differ significantly between males and females ($P>0.05$), these data for the two sexes were pooled. The relationship between weight and fork length for both sexes combined was described by the equation

$$\log W = \log 1.22x\ 10^{-5} + 3.06 \log FL \quad (n=1026,\ r^2=0.99).$$

Validation of aging method

The mean monthly marginal increments on sectioned otoliths of western butterfish with one, two, three, and four–seven opaque zones reached their maxima in October, after which they declined markedly to their minima in either November or December and then rose progressively over the ensuing months (Fig. 1). The pronounced decline and then progressive rise, exhibited by the mean monthly marginal increments on the otoliths of western butterfish, irrespective of the number of opaque zones, demonstrates that a single opaque zone is formed in the otoliths of *P. vitta* each year and that the number of such zones can thus be used to age this species accurately.

Growth

The von Bertalanffy growth curve provided a good fit to the fork lengths at age of the females and males of *P. vitta* (Fig. 2). This good fit is reflected in the high coefficients of determination (r^2) of 0.942 for females and 0.924 for males and by the values for t_0 being close to zero (Table 1). The von Bertalanffy growth curves of the females and males of *P. vitta* in Shark Bay differed significantly ($P<0.05$), and the difference in L_∞ between females and males contributed more to the difference than that of either k or t_0.

Females were more prevalent than males in length classes below 160 mm, whereas the opposite was true above this length (Fig. 3A). However, age-frequency distributions showed that females were more prevalent in all age classes (Fig. 3B). The overall sex ratio was 1.4 females:1 male.

Reproductive biology

Because virtually all *P. vitta* became mature at the end of their first year of life, the GSIs for all fish ≥1 year

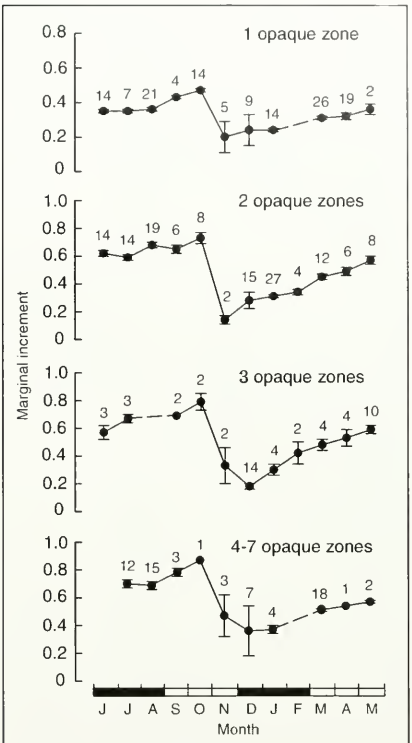

Figure 1

Mean monthly marginal increments (±1 standard error) for sagittal otoliths of the western butterfish (*Pentapodus vitta*), derived from samples collected between 1999 and 2004. Sample size is given for each month. The closed rectangles represent the summer and winter months and the open rectangles the autumn and spring months.

of age were calculated. The mean monthly GSIs for female western butterfish remained low (<0.9) in winter (June to August) and early spring (September), but then increased sharply from September to reach a maximum of 4.0 in late spring (November), before declining markedly during mid-summer (January) (Fig. 4). Although the pronounced seasonal trend displayed by the mean monthly GSIs for males was very similar to that for females, the maximum mean monthly GSI of males was approximately one tenth of that for females.

All female western butterfish that were ≥1 year old and caught between February and August (apart from a few in July) possessed ovaries at stage I or II (i.e., they were virgin or immature; Fig. 5). Females with

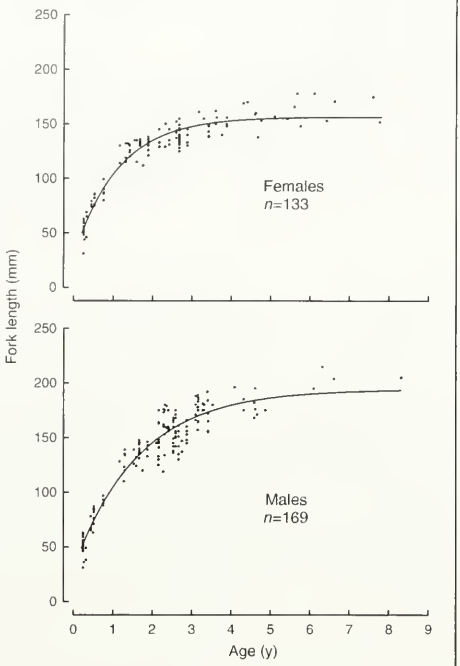

Figure 2

Von Bertalanffy growth curves fitted to fork lengths at age for individual females and males of western butterfish (*Pentapodus vitta*).

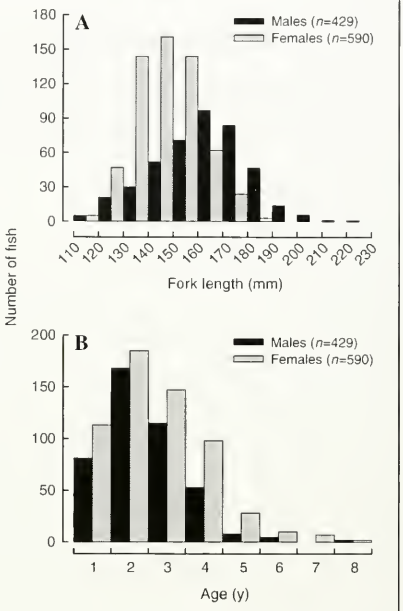

Figure 3

(**A**) Length-frequency and (**B**) age-frequency distributions for males and females of western butterfish (*Pentapodus vitta*).

Table 1

Von Bertalanffy growth parameters and their upper and lower 95% confidence limits for females and males of the western butterfish (*Pentapodus vitta*) in Shark Bay. r^2= coefficient of determination; n=number of fish in sample.

Sex	Confidence intervals	k (/year)	L_∞ (mm FL)	t_0 (years)	r^2	n
Females	Estimate	0.886	156.6	−0.233	0.942	133
	Upper	0.928	159.2	−0.058		
	Lower	0.844	154.0	−0.408		
Males	Estimate	0.602	194.4	−0.282	0.924	169
	Upper	0.624	197.9	−0.189		
	Lower	0.580	190.9	−0.375		

stage-III (developing) and stage-IV (maturing) ovaries were first found in July and were also present in September. Fish with stage-V (prespawning) and stage-VI (spawning) ovaries collectively dominated the samples obtained in October to December and were still the most prevalent group in January. The samples in January also contained one fish with stage-VIII (recovering spent) and some with stage-II ovaries but none with ovaries at stages III or IV (Fig. 5). The above trends provide strong evidence that any female with ovaries

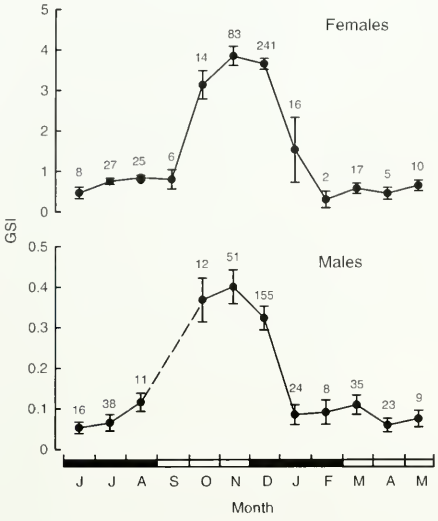

Figure 4

Mean monthly gonadosomatic indices (GSI) (±1 standard error) for females and males of western butterfish (*Pentapodus vitta*) that were ≥1 year old. Monthly sample sizes are given above each mean.

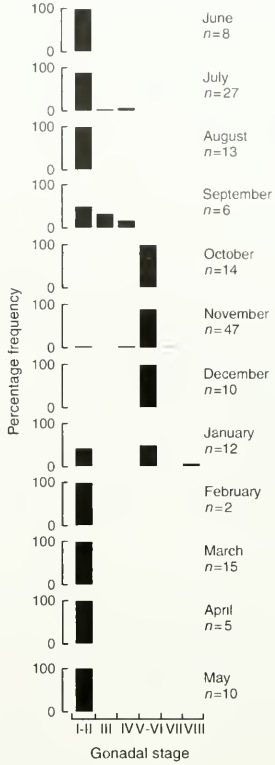

Figure 5

Histograms showing percent frequency of occurrence of each of the various gonadal stages in female western butterfish (*Pentapodus vitta*) in each month of the year.

that had developed to at least stage III by September would have progressed through to maturity during the ensuing months of the spawning period if it had not been removed from the population.

In each month, the distribution of oocyte diameters in the mature ovaries of *P. vitta* produced a well-defined mode between ~20 and 80 μm, which represented chromatin nucleolar- and perinucleolar-stage oocytes. Cortical alveolar oocytes were present in some ovaries in July and September, when oocyte diameters had reached a maximum of 200 and 150 μm, respectively. These larger oocytes and also yolk granule oocytes were abundant between October and December and reached a maximum diameter of 380 μm. The contribution of cortical alveolar and yolk granule oocytes declined in January. Hydrated oocytes were found in several ovaries in October, December, and January and postovulatory follicles were present in some ovaries during November.

Mortality

The age-frequency distributions for both female and male western butterfish caught during extensive trawling in November and December of 1997 had a modal peak at 2 years of age (Fig. 3B). Because the age at full recruitment was thus considered to be 3 years, catch curve analysis was undertaken with data for the 3+ and older age classes. The resulting point estimate for the instantaneous rate of total mortality, Z, was significantly greater ($P<0.05$) for males (1.15/year) than for females (0.91/year) (Table 2). Likewise, the simulation method of Hall et al. (2004), based on the number of individuals above 5 years of age (2 males and 13 females for sample sizes of 130 and 253, respectively), yielded a greater point estimate of Z for males (1.34/year) than females (0.89/year). The point estimate for Z, derived by inserting the maximum ages for female and male butterfish (8 years for both males and females), into the refitted Hoenig (1983) equation for fish, was 0.55/year for the two sexes (Table 2). The point estimates for the

instantaneous rate of natural mortality, M, derived by inserting the parameter values for western butterfish into the refitted Pauly (1980) equation, were higher for females (1.78/year) than males (1.28/year).

The combined point estimate for Z derived using the method of Hall et al. (2004) was greater for males (1.14/year) than females (0.89/year; Fig. 6). This method yielded a slightly higher point estimate of M for males (0.80/year) than females (0.71/year) (Fig. 6).

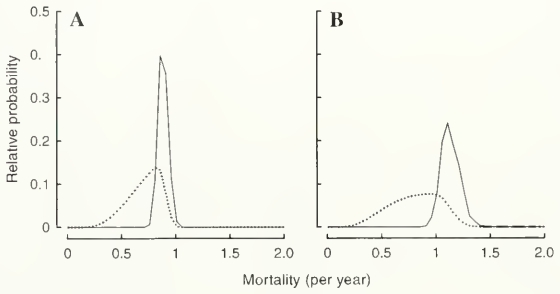

Figure 6

Combined posterior probability distributions for Z (solid line) and M (dotted line) for (**A**) females and (**B**) male western butterfish (*Pentapodus vitta*).

Discussion

Validation of aging method, age composition, and growth

The validation that the opaque zones of *P. vitta* are formed annually, together with the very high repeatability of their counts in sectioned otoliths, demonstrate that the number of these opaque zones (annuli) in sectioned otoliths can be reliably used for aging this nemipterid. Stephenson and Hall (2003) demonstrated that the annuli in sectioned otoliths of another nemipterid, *Nemipterus furcosus*, in Western Australia are also formed annually.

The vast majority of the *P. vitta* caught in Shark Bay were less than seven years old and the oldest individual was just over eight years old. The pattern of growth for females and males differed. Thus, the males of each age were, on average, larger than females after the first year of life and had a greater L_∞. However, most of the growth of both sexes occurs during the first three years of life.

Spawning period

The highly elevated mean monthly GSIs of females and males between October and December and the restriction of females with mature ovaries to the period between

Table 2

Point estimates and their 95% confidence intervals for total mortality, Z, and natural mortality, M, for the western butterfish (*Pentapodus vitta*), calculated by using life history models, estimation of longevity based on simulation, catch curve analysis and Bayesian analysis. Methods used for main interpretations of mortality are in bold.

Method of analysis	Z or M (/year)	Point estimate	Lower 95% CI	Upper 95% CI
Males				
Catch curve analysis	Z	1.15	0.96	1.33
Simulation (number of fish >5 years old)	Z	1.34	0.90	1.95
Refitted Hoenig (1983) fish equation	Z	0.55	0.19	1.52
Combined Z (Bayesian method)	**Z**	**1.14**	**1.01**	**1.35**
Refitted Pauly (1980)	M	1.28	0.42	3.91
Combined M (Bayesian method)	**M**	**0.80**	**0.37**	**1.23**
Females				
Catch curve analysis	Z	0.91	0.78	0.99
Simulation (number of fish >5 years old)	Z	0.89	0.69	1.11
Refitted Hoenig (1983) fish equation	Z	0.55	0.19	1.52
Combined Z (Bayesian method)	**Z**	**0.89**	**0.82**	**1.01**
Refitted Pauly (1980)	M	1.78	0.56	5.35
Combined M (Bayesian method)	**M**	**0.71**	**0.39**	**0.97**

October and January implies that *P. vitta* spawns during these latter four months. This conclusion is consistent with hydrated oocytes or postovulatory follicles or a combination of both being found only in fish caught between October and January. Furthermore, the precipitous decline in the mean monthly GSIs between December and February and the presence of only stage-II ovaries in February strongly indicates that spawning does not extend into this month. Because spawning activity peaked between October and January, the western butterfish was given a birth date of 1 December when an age was assigned to each fish. Because mature ovaries of *P. vitta* often contained a relatively wide size range of vitellogenic oocytes and, in many cases, also either hydrated oocytes or postovulatory follicles, this species is considered a multiple spawner *sensu* deVlaming (1983), namely individual females release eggs on more than one occasion in a spawning season.

Is there evidence that *Pentapodus vitta* is hermaphroditic?

Our data demonstrate that, in the population of *P. vitta* in Shark Bay, the females are relatively more abundant than males in length classes below 160 mm, whereas the reverse is true of length classes above that length (Fig. 3A). In contrast, the prevalence of females was always greater than that of males in each age class. The trend towards an increasing prevalence of males vs. females with increasing body length can thus be attributed to the males growing faster. The fact that there was not a progressive shift towards an increase in one sex with increasing age and none of the gonads of the 178 fish examined contained both ovarian and testicular tissue provides overwhelming circumstantial evidence that *P. vitta* is gonochoristic. Like *P. vitta*, other nemipterid species also exhibit a size-related skew in their sex ratios that can be explained by differences in growth rates between the two sexes (e.g., Young and Martin, 1985; Lau and Sadovy, 2001; Raje, 2002; Granada et al., 2004). The trend among gonochoristic nemipterids, for their males to grow larger than their females, presumably reflects a selective advantage of being large during courtship or mating (Granada et al., 2004). In contrast to these gonochoristic species, some nemipterids are protogynous hermaphrodites, e.g., *Scolopsis monogramma, S. taeniopterus* and *S. bilineatus* (Young and Martin, 1985).

Mortality

The point estimates for natural mortality, M, derived for males and females of *P. vitta* with Pauly's (1980) equation, were inconsistent with the point estimates derived for total mortality, Z. This conclusion is drawn from the fact that the point estimates for M were greater than those for Z from both Hoenig's (1983) equation for fish and catch curve analysis, thereby paralleling the situation with several other species (see Hall et al., 2004), and also those derived from the simulation and Bayesian methods of Hall et al. (2004). The use of the method of Hall et al. (2004) reconciled the inconsistencies between M and Z for *P. vitta* and provided more precise estimates, particularly for M. Because the point estimates for Z were only slightly greater than those for M, the population of *P. vitta* in Shark Bay does not appear to have been subjected to heavy fishing pressure. In this context, it is relevant that, because the vast majority of *P. vitta* attain maturity by the end of their first year of life, most individuals will have had the opportunity to spawn at least twice before they become fully recruited into the trawl fishery. Furthermore, recreational anglers return about 73% about of the western butterfish they catch in Shark Bay live to the water (Sumner et al.[2]).

Pentapodus vitta lives for up to eight years, but grows very rapidly early in life and attains maturity by the end of the first year of life. The males of *P. vitta* grow more rapidly and reach a larger size than their females. The western butterfish is a gonochoristic species that, in Shark Bay, spawns between mid-spring and mid-summer. Although commercial and recreational fishermen obtain large numbers of *P. vitta* as bycatch in Shark Bay, this fishing does not appear to have a marked impact on the numbers of this very abundant species in this large subtropical embayment.

Acknowledgments

Gratitude is expressed to many colleagues in the Department of Fisheries, Western Australia, and the Centre for Fish and Fisheries Research, Murdoch University for help with sampling. Comments and constructive criticisms were kindly provided by Michael Mackie, Peter Stephenson, and Gary Jackson. Financial and technical assistance were provided by the Department of Fisheries, Western Australia, and Murdoch University.

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The use of multibeam sonar mapping techniques to refine population estimates of the endangered white abalone (*Haliotis sorenseni*)

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Abstract—Multibeam sonar mapping techniques provide detailed benthic habitat information that can be combined with the data on species-specific habitat preferences to provide highly accurate calculations of populations in a particular area. The amount of suitable habitat available for the endangered white abalone (*Haliotis sorenseni*) was quantified to aid in obtaining an accurate estimate of the number of remaining individuals at two offshore banks and one island site off the coast of southern California. Habitat was mapped by using multibeam sonar survey techniques and categorized by using rugosity and topographic position analysis. Abalone densities were evaluated by using a remotely operated vehicle and video transect methods. The total amount of suitable habitat at these three sites was far greater than that previously estimated. Therefore, although present estimates of white abalone densities are several orders of magnitude lower than historic estimates, the total population is likely larger than previously reported because of the additional amount of habitat surveyed in this study.

Manuscript submitted 2 May 2005
to the Scientific Editor's Office.

Manuscript approved for publication
6 December 2006 by the Scientific Editor.

Fish. Bull. 104:521–532 (2006).

Accurate classification of habitat is important for examinations of the distribution and abundance of marine organisms. The potential complexity of species-habitat relationships is such that the use of a single parameter when trying to link species to specific areas has become obsolete. Multiple physical oceanographic parameters that link species to their habitat have proven to be useful, although they are not applicable to all types of marine organisms (Freeman and Rogers, 2003). The use of high-resolution multibeam sonar maps for classifying habitat has become a critical step in the process of estimating the distribution and abundance of marine animals that are known to be associated with particular habitat types. Because an increasing number of marine resources are in states of decline, information on the amount of habitat of specific types and qualities becomes crucial to making predictions for the purposes of fisheries management, and to aid in decisions concerning potential locations of marine protected areas (Kvitek et al.[1]; Iampietro et al., in press). For species in states of decline, protection of known critical habitat may be the only approach available to enhance survival of the species. Detailed habitat mapping provides a large amount of information on the benthic makeup of an area in a relatively short amount of time, and further processing of data with GIS (geographic information system) can produce accurate estimates of actual areas categorized by various physical parameters. These pieces of information, coupled with field surveys to obtain information on animal or plant habitat associations,

[1] Kvitek, R., P. Iampietro, C. Bretz, K. Thomas, S. Zurita, B. Jones, and E. Morris. 2004. Hydrographic data acquisition in support of MLPA and MLMA Implementation. California Department of Fish and Game Final Report P0170015, p. 1–74. Foundation of California State University Monterey Bay, 100 Campus Center, Seaside, CA 93955.

can allow for detailed and accurate estimates of abundance of marine organisms.

The white abalone (*Haliotis sorenseni*) is one of six abalone species (red, green, pink, pinto, black, and white) that have been exploited commercially on the west coast of North America. The species ranged historically from Morro Bay, California, USA, to Punta Rompiente, Baja California, Mexico (Geiger, 1999). Serial depletion of stocks of congeneric, relatively shallow-dwelling abalone species led to the exploitation of white abalone, the deepest living abalone species in the North Pacific (Karpov et al., 2000). During a ten-year period from 1969 to 1978, approximately 360,000 white abalone were harvested (Hobday et al., 2001). After 1978, the mandatory reporting of white abalone landings was no longer required, and although abalone fishing effort has remained high, there are (at present) no data on the numbers taken (Tegner, 1989).

In surveys conducted in the late 1990s in suitable habitat, very low numbers of white abalone were reported (Davis et al., 1996, 1998; Haaker et al.[2]; Hobday et al., 2001). Densities at many localities were less than 1 abalone/ha, and the entire population of white abalone was estimated at less than 3000 individuals (Hobday et al., 2001). Reproductive efforts of the remaining adults are believed to have been seriously hindered by potential Allee effects (Allee, 1931) because of low densities. Concern for the survival of the species prompted a status review and the white abalone was listed as an endangered species by the Department of Commerce on 29 May 2001 (Federal Register, 2001).

Postexploitation estimates of abundance and available white abalone habitat need revision because the spatial coverage of sampling in the 1980s and 1990s was limited in the case of determining abundance estimates and virtually nonexistent in the case of determining habitat classification (Lafferty et al., 2004). Accurate estimates of density and the amount of suitable habitat are critical for making informed decisions regarding how to prioritize recovery actions and where to focus population enhancement efforts. In addition, identification of the specific locations of white abalone in the wild will help both to focus efforts to protect areas where the species remain and to locate potential brood stocks for captive breeding. Information on the recruitment potential of the remaining individuals cannot be directly assessed, but an examination of the temporal trends in size distributions may be helpful in addressing questions of population viability and sustainability. The present study was conducted with recovery efforts in mind, and therefore included intensive sampling of offshore banks and islands where white abalone abundance was high historically. We used a combination of advanced mapping technology (multibeam sonar and side-scan sonar) and a remotely operated vehicle (ROV) to quantify the total amount of available habitat at each location, in order to examine the size distributions of surviving populations, and to derive new estimates of white abalone abundance.

Materials and methods

Habitat mapping

Habitat was surveyed during three cruises on the NOAA ship RV *David Starr Jordan* at Tanner Bank (July 2002 and September 2004), Cortes Bank (July 2003), and San Clemente Island (August 2004) with multibeam (all years, Fig.1) and side-scan sonar techniques (2002 only). The multibeam sonar system, which was installed on the RV *David Starr Jordan* for the Tanner Bank 2002 and Cortes Bank 2003 cruises, included a Reson 8101 multibeam sonar (Reson Inc. Goleta, CA) supplemented with a side-scan sonar option, and was used in conjunction with a Triton-Elics Isis System (Triton Elics International, Portland, OR) for data logging and sonar control. The San Clemente Island 2004 habitat survey was conducted by using the same sonar system aboard a smaller vessel, the RV *VenTresca*, in conjunction with ROV operations conducted aboard the RV *David Starr Jordan*. Delphmap and BathyPro software (Triton Elics International, Inc., Portland, OR) were used to create real-time side-scan mosaics and to generate digital elevation models. The pitch and roll motion of the vessel used for mapping was corrected for using a TSS HDMS (heading and dynamic motion sensor) (pitch, roll and heading accuracy ±0.02°; heave accuracy ±5% or 5 cm). Hypack Max software (Hypack, Inc., Middletown, CT) was used for survey planning and navigation. Positioning information was provided by a Trimble 4700 GPS receiver and NavBeacon for receiving U.S. Coast Guard RTCM (radio technical commission for maritime communications) corrections. Sound velocity profile data were collected with an Applied Microsystems (Sydney, British Columbia, and CA) SVPlus sound velocimeter. Multibeam data were processed with CARIS HIPS software (CARIS USA, Ellicott City, MD), and all final GIS products were derived from shoal-biased data.

Microhabitat analysis

Habitat type and algal cover were examined for surveys conducted at Tanner Bank in 2002. Habitat was characterized by broad type (e.g., bank, seamount), modifiers (e.g., faulted, eroded), microhabitat (e.g., sand, boulders), seafloor slope (by degree), seafloor complexity (5 levels), and algal cover (species identification and four levels of coverage), after Greene et al. (1999; Table 1).

Abalone surveys

Abalone surveys were conducted with a Phantom HD 2 + 2 (2002 and 2003) and a Phantom DS4 (2004)

[2] Haaker, P. L., D. V. Richards, and I. Tanaguchi. 2000. White abalone program October 9–25, 1999, cruise report, p. 1–17. California Department of Fish and Game, 330 Golden Shore Suite 50, Long Beach, CA 90802.

Table 1

Habitat analysis variable descriptions (Greene et al., 1999). Only those classifications that were used frequently enough to influence the PCA write out are listed (a total of 12 were included in the analysis). For algal levels, coverage was defined by the following within the video-captured field of view: absent = <10%, rare = 10–35%, present = 35–75%, and highly abundant = 75–100%.

Variable abbreviation	Variable type	Levels
Mhab 1–4	Macro/Microhabitat	1=boulders; 2=deformed (faulted or folded); 3=deformed (faulted or folded) + boulders; 4=deformed (faulted or folded) + sand
Slope 1 and 2	Seafloor slope	1=flat (0 to 1 degree); 2=sloping (1 to 30 degrees)
Com 1 and 2	Seafloor complexity	1=very low complexity; 2=low complexity
Br 1–4	All brown algae	1=absent; 2=rare; 3=present; 4=highly abundant
L 1–4	*Laminaria farlowii*	1=absent; 2=rare; 3=present; 4=highly abundant
A 1–4	*Agarum fimbriatum*	1=absent; 2=rare; 3=present; 4=highly abundant
E 1–4	*Eisenia arborea*	1=absent; 2=rare; 3=present; 4=highly abundant
D 1–4	*Dictyotaceae* spp.	1=absent; 2=rare; 3=present; 4=highly abundant

remotely operated vehicle (ROV) equipped with a forward-looking 12:1 zoom color video camera (all surveys) and a high resolution Nikon Coolpix digital still camera (2004 surveys only, Insite Pacific Inc., Solana Beach, CA). We recorded video footage continuously on digital tapes and overlaid footage with temperature, depth, heading, and time information from an on-screen display. Two pairs of lasers were mounted near the front of the ROV in parallel: one pair to measure abalone upon sighting (10.0 cm apart), and one pair to estimate the search field of view (60 cm apart). Upon sighting an abalone, the ROV pilot maneuvered the vehicle into position to zoom in on and photograph the animal for species confirmation, ensuring that the narrow pair of lasers passed over the abalone so that a size estimate could be obtained. Empty abalone shells were also noted and identified.

The ROV was tracked by using a directional hydrophone mounted on the ship and a transponder mounted on the ROV. Positional data and all other navigational and physical data associated with the ROV dives (e.g., heading, depth, and water temperature) were recorded every two seconds. Because of the great depth range that white abalone inhabit, it was not logistically feasible to compare ROV transect observations with diver transect observations. It is possible that we missed abalone residing on the back sides of rocks as the ROV passed over.

Sampling design and site selection

Multibeam and side-scan surveys were conducted the preceding night at sites that were to be surveyed with the ROV during the next day. Transect locations were chosen randomly initially, but after preliminary surveys at Tanner Bank revealed a narrow depth range of abalone occurrence from 30 to 60 m and a habitat restriction to rock reef or the sand-and-rock reef interface, only areas of suitable habitat (depths ranging from 30 to 60 m [±5 m]) were surveyed. In general, we attempted to run transects for approximately two hours, and to a length of 1 km, although actual lengths were calculated after the dive. Several of the early surveys included transects of greater lengths of time and distances. Georeferenced bathymetry maps were interfaced with the ROV navigational software for all dives, allowing for the ship, and in effect the ROV, to remain within a particular depth stratum and within suitable habitat.

Postdive processing

Videotapes and still photos were reviewed to confirm species identification, measure sizes, search for additional abalone, record search effort, examine microhabitat, and determine the search field of view. Other abalone species that were encountered were noted (red and pink). We used strip transect techniques to estimate densities, and therefore the field of view was measured for abalone sightings from the first survey (Tanner Bank, 2002), and the average (2 m [±0.85 SD], n=171) was used as the strip width for the entirety of each transect in the study.

Data analysis

For habitat classification a statistical approach called textural analysis (described in Cochrane and Lafferty, 2002) was used to identify complex rock areas at Tanner Bank as documented by side-scan sonar (Fig. 1, A and B). We estimated the total area of available white abalone habitat on each bank by calculating the amount of rocky substrate in depth intervals, as determined by multibeam sonar surveys. A combination of rugosity and topographic position analysis (TPI) were used

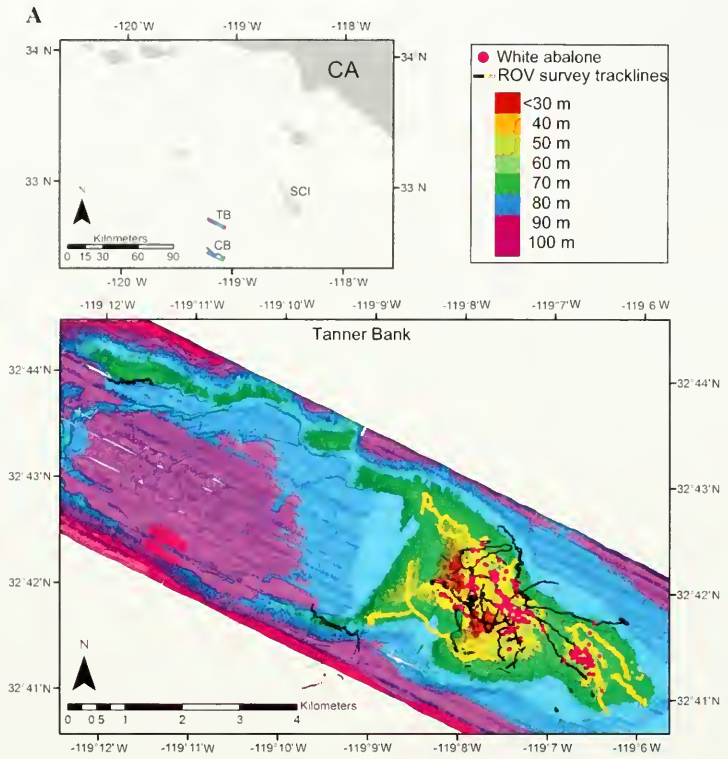

Figure 1

(**A**) High-resolution bathymetry of Tanner Bank and map of the southern California coast. Black lines represent ROV transect track lines in 2002 and yellow lines represent track lines in 2004. Pink dots on track lines represent white abalone (*Haliotis sorenseni*) sightings. Depth strata are distinguished by color (see legend). CA=California; SCI=San Clemente Island; TB=Tanner Bank; CB=Cortes Bank. (**B**) High-resolution bathymetry of Cortes Bank and San Clemente Island. Black lines represent ROV transect track lines. Pink dots on track lines represent white abalone (*Haliotis sorenseni*) sightings. Depth strata are distinguished by color (see legend).

for multibeam habitat classification (Kvitek et al.[3]). A rugosity measure was used to evaluate the "texture" of the seafloor by quantifying the surface area to planar area. Rugosity calculations were done with ArcView 3.2 (ESRI, Redlands, CA) by using the "Surface Area and Ratios from Elevation Grid , vers 1.2." (Jenness, 2002). Rugosity measures ranged from 1 to 4, and higher values indicated more texture (i.e., rocky terrain). TPI was calculated in ArcGIS, vers. 8.3 by a multistep process. For each cell the focal mean of the digital elevation model (DEM) was calculated to compute an average depth value used to obtain a measure of relative elevation. Relative elevations were classified into six TPI classes to allow for visual representation of elevations. Bottom types were noted during ROV surveys and compared to bottom types determined by sonar data, and in all cases results were confirmed.

Principal component analysis (PCA) was used to examine potential relationships between habitat type and

[3] Kvitek, R. G., P. J. Iampietro, and E. Summers-Morris. 2003. Integrated spatial data model tools set for the auto-classification and delineation of species-specific habitat maps from high-resolution, digital hydrographic data. Report prepared for NOAA National Ocean Service (NOS), p 1–74. NOAA Coastal Services Center, 2234 South Hobson Ave., Charleston, SC 29405.

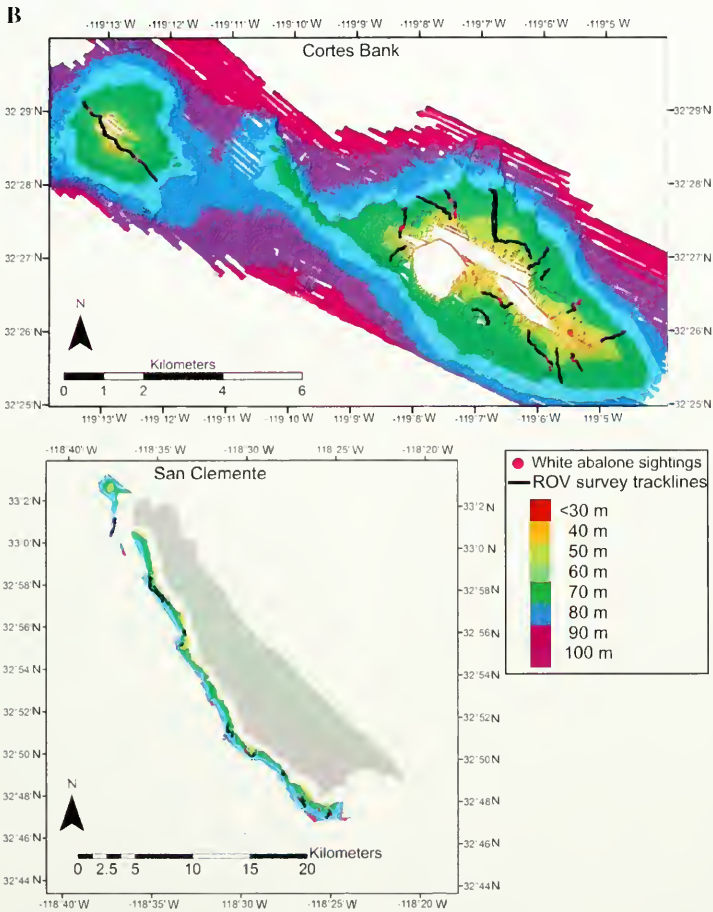

Figure 1 (continued)

algal cover in segments containing abalone, and those where abalone were absent for the Tanner Bank 2002 survey. For the purposes of PCA, transects were divided into 100-m segments. All PCA coefficients were plotted initially to examine relationships between abalone presence and absence and defined variables. Coefficients from the most influential variables were then plotted to examine these relationships more closely.

Transects varied in length from 0.4 to 6 km, although most transects were close to 1 km in length. To estimate abalone densities we attempted to search within a particular 10 m depth interval during each transect. When this was not possible, transects were poststratified by depth interval (10 m), because results of preliminary surveys provided evidence of the prevalence of white abalone within particular depth ranges. For the few cases (2) where poststratification yielded a search area of less than 100 m^2, the data for these areas were excluded from the analysis because densities would be artificially inflated. We calculated density per unit of area for each transect and stratified transects by three depth intervals (30–40 m, 40–50 m, and 50–60 m) to test for differences among depths and sites using Kruskal-Wallis nonparametric techniques on ranked data (Systat vers. 11, Systat Software Inc., Point Richmond, CA). The mean depth of abalone occurrence was tested

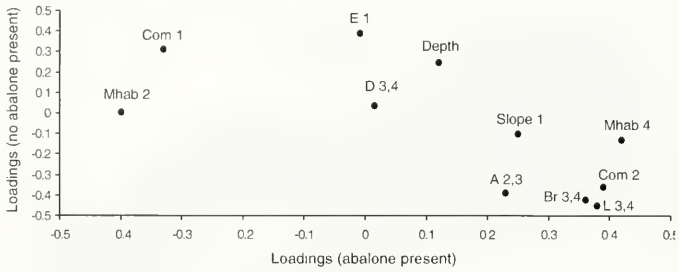

Figure 2

Summary results of principal component analysis for the 2002 Tanner Bank survey with white abalone (*Haliotis sorenseni*) present (*x*-axis) and no white abalone present (*y*-axis). See Table 1 for abbreviations and habitat descriptions.

for differences among sites with a one-way ANOVA. Depth and size distributions were compared among sites with a Kolmogorov-Smirnov (K-S) test. To estimate population sizes at each site, densities were applied to depth-area polygons derived from multibeam sonar bathymetry.

To examine the fine-scale spatial distribution of white abalone on the banks we determined and plotted linear distances between individuals along transects and recorded the number of groups (individuals within 2 m of another abalone) versus individuals (no other abalone within 2 m). Additionally, the distances between all individuals at each site were calculated, and for each abalone the distance to the nearest subsequent abalone sighting was determined. This was not a traditional nearest neighbor analysis, because transects were not designed for such an analysis. To test the degree of dispersion of the population on a broader scale, the cumulative number of white abalone observed within 250-m^2 segments of transect between 40 and 50 m depth (the depth range with the highest abalone densities) at Tanner Bank in 2002 were fitted to a negative binomial distribution (Elliott, 1977). The Tanner Bank 2002 surveys were appropriate for this analysis because of the high number of abalone sightings there.

Results

Habitat

The amount of rocky habitat between 30 and 60 m depth at Tanner Bank, Cortes Bank, and the west side of San Clemente Island was 1359, 1139 and 889 ha, respectively (Fig. 1). Side-scan sonar data indicated that the majority of the sea floor shallower than 60 m at all sites is hard substrate (Fig. 1). High-resolution bathymetry from multibeam sonar revealed a complex structure on the offshore banks. Tanner Bank and Cortez Bank are uplifted anticlines that have been eroded by wave action from the northwest during past periods of lower sea level (Vedder et al., 1986). Erosion of more recent geologic units has exposed erosion-resistant marine sedimentary and volcanic rocks that through differential erosion have developed layering and fracture features favorable to abalone. San Clemente Island is on the uplifted southern side of the San Clemente fault (Vedder et al., 1986), and is composed of erosion-resistant volcanic rocks of the same age as those at Tanner and Cortez Banks.

Microhabitat analysis

At Tanner Bank in 2002, white abalone were generally found in association with two species of brown algae (*Laminaria farlowii* and *Agarum fimbriatum* [88% of white abalone sightings included one or both species]), a foliose red alga (*Rhodymenia* spp. [45% of sightings]), geniculate coralline algae (*Calliarthron* spp.) and *Corallina* spp. [79% of sightings]), and encrusting coralline algae (*Lithothamnion* spp. [100% of sightings]). The brown alga *Dictyotaceae* spp. was present in 9% of white abalone sightings (mostly in deeper waters), and *Eisenia arborea* in 6% of sightings (mostly in shallower waters).

A PCA examination of these data revealed a strong positive relationship between the presence of white abalone and several factors; the strongest loadings occurred with depth, microhabitat type (Mhab 4 (deformed with sand)), the magnitude of seafloor slope (slope 1, flat), moderate seafloor complexity (Com 2 (low)), and the relative abundance (common or abundant) of brown algae A (*Agarum fimbriatum*), L (*Laminaria* spp.), and Br (brown algae spp. in general); (Fig. 2, Table 1). In contrast, a strong negative relationship existed between zero white abalone density and habitat characteristics; the strongest negative relationships occurred with the frequent presence of various algal species (same as above). There were strong positive relationships

between zero white abalone density and the presence of *Eisenia arborea*, and zero white abalone density and low seafloor complexity (com 1 [very low]).

Although detailed habitat analyses were not completed for the 2003 Cortes Bank survey, we noted the presence of the brown algae *Pterygophora californica* and *Cystoseira* spp. (both absent at Tanner Bank in 2002), and the apparent absence of *Dictyotaceae* spp. in deeper waters.

Abalone abundance, depth, and size distribution

A total of 258 individual white abalone were identified in all surveys, and the highest numbers were seen at Tanner Bank in 2002 (19.8 abalone/ha, Fig. 3, Table 2). Densities ranged from 0.0 abalone/ha (San Clemente Island, 50–60 m depth range) to 19.8 abalone/ha (Tanner Bank 2002, 40–50 m depth range, Fig. 3, Table 2). Very few individuals of other haliotids (5 pink and 3 red) were identified. Search effort was focused on the 30–60 m depth range after preliminary results at Tanner Bank indicated that white abalone inhabit this depth range, but surveys were conducted at shallower and deeper depths at each site to confirm these findings. No abalone were found shallower than 32 m or deeper than 61 m at any site, and therefore the results of these surveys were not included in the analysis. Overall densities differed significantly between surveys (n=162, Kruskal-Wallis test, test statistic=23.76, P<0.0001). Densities within surveys grouped by 10 m depth bins only differed significantly by depth for the Tanner Bank 2002 survey (n= 33, Kruskal-Wallis test, test statistic=10.45, P<0.01, Fig. 3). The total number of abalone shells ranged from 44 (San Clemente Island) to154 (Cortes Bank). The depth distribution of white abalone for all surveys combined reveals that white abalone were stratified by depth overall, although search effort was focused on the middle depth ranges (Figs. 3 and 4). The depth distribution of empty shells was similar to that of live white abalone (31–61 m), although there were several (<10) shells found

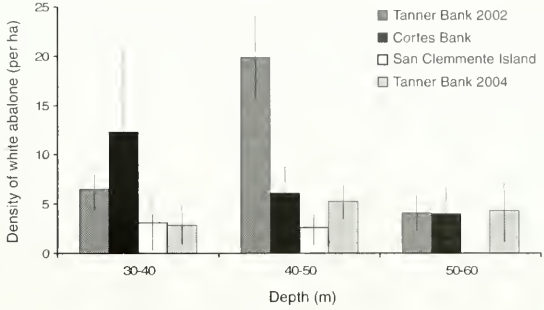

Figure 3

Density of white abalone (*Haliotis sorenseni*) by depth at Tanner Bank (two years), Cortes Bank, and San Clemente Island. Error bars represent standard error.

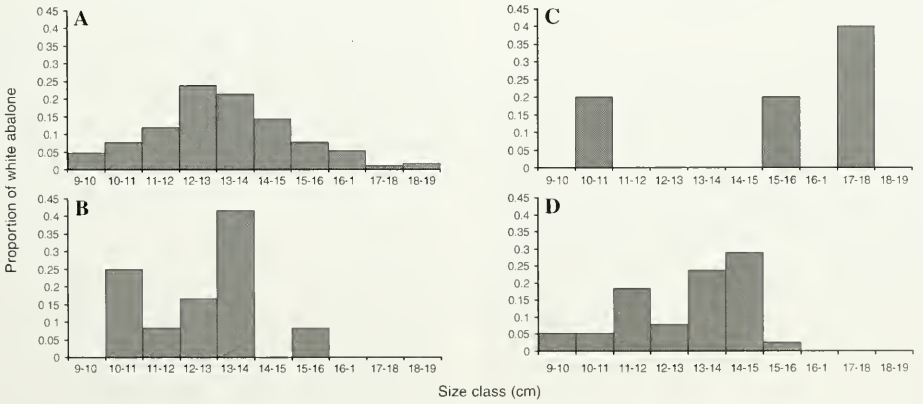

Figure 4

Size distribution for white abalone (*Haliotis sorenseni*) at (**A**) Tanner Bank, 2002 (n=168), (**B**) Cortes Bank (n=12), (**C**) San Clemente Island (n=5), and (**D**) Tanner Bank, 2004 (n=35).

Table 2

Density of white abalone (*Haliotis sorenseni*), area surveyed by the ROV, habitat area and population estimates by depth strata for Tanner Bank, Cortes Bank, and San Clemente Island.

	Tanner Bank			
Depth (m)	Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population
30–40	2002: 6.5 ±2.1 2004: 2.9 ±1.9	2002: 3.5 2004: 0.93	245	2002: 1592.5 ±514.5 2004: 710.5 ±465.5
40–50	2002: 19.8 ± 4.3 2004: 5.2 ± 1.7	2002: 5.0 2004: 3.9	425	2002: 8415.0 ±1827.5 2004: 2210.0 ±722.5
50–60	2002: 4.08 ±1.8 2004: 4.3 ±3.1	2002: 2.3 2004: 1.7	689	2002: 2811.1 ±1240.2 2004: 2962:7 ±2135.9
Total	2002: 13.0 ±3.5 2004: 6.1 ±1.5	2002: 10.8 2004: 6.5	1619	2002: 12,818.6 ±3582.2 2004: 5883.2 ±3323.9

at relatively shallow (<25 m) and one shell found at a relatively deep depth (72 m).

The sizes of white abalone at all sites ranged from 9.0 to 19.0 cm (Fig. 4). No small abalone were observed, although turban snails smaller than 6 cm were detected by using ROV sampling methods. Size distributions differed significantly for comparisons made between Tanner Bank 2002 and Cortes Bank, and Tanner Bank 2002 and San Clemente Island (K-S test, $P<0.01$, Fig. 4). There was an apparent shift in size distributions between years at Tanner Bank; fewer large animals were found in 2004 than in 2002, although the overall size distributions did not differ significantly between years (K-S test, $P=0.19$, Fig. 4). The size distribution at Cortes Bank included animals in the mid size range, and no abalone in the smallest or largest size ranges. Densities at San Clemente Island were too low to show any real pattern in size distribution (Fig. 4). The mean size of abalone ranged from 12.4 cm to 13.7 cm and did not differ significantly between surveys (ANOVA, $P>0.05$).

Site-specific white abalone population estimates were based on the amount of available habitat quantified from the results of multibeam sonar surveys and white abalone density estimates determined from data from ROV surveys. The total population of white abalone on Tanner Bank based on 2002 density measurements was estimated at 12,819 ±3582 (SE), whereas the total population estimate based on 2004 density measurements was 5883 ±3324. The total population on Cortes Bank was estimated at 7366 ±5340 (SE), and that at San Clemente Island was estimated at 1938 ±1598 (SE; Table 2).

White abalone reproductive potential

Eighty-nine percent of white abalone at all sites were observed as singletons, and only 6% were observed in groups. Group sizes ranged from two to five individuals and the largest group was observed at Tanner Bank in 2002. There were no sightings of abalone in groups at Tanner Bank in 2004. White abalone were not found frequently in groups during any of the surveys, and the observed number of individuals within 250-m^2 subsamples within the 40–50 m depth range at Tanner Bank in 2002 did not differ from values predicted by the negative binomial distribution (chi-square=4.9, $P=0.67$).

The results of an analysis of distances between sightings indicated that less than 25% of individual abalone were located within 5 m of one another for all surveys. The majority of individuals (60%) were over 20 m away from another sighted abalone. The survey with the highest proportion of abalone located within a distance of 20 m of another individual was that at Tanner Bank in 2002. In regard to potential mating pairs, out of a possible 19,503 combinations of mating pairs, only 202 were within 30 m from one another at Tanner Bank in 2002, 4 out of 231 pairs at Cortes Bank, 3 out of 12 pairs at San Clemente Island, and 10 out of 861 pairs at Tanner Bank in 2004.

Discussion

Few areas in U.S. waters have been adequately mapped to reveal detailed bathymetry or substrate characteristics. Consequently, our knowledge of the amount of habitat available for benthic marine organisms is so inadequate that one can only speculate about overall population sizes. White abalone populations in southern California are no exception; all previous estimates of the amount of suitable habitat available for white abalone have been based on the assumption made by Thompson et al. (1993) that 3% of the sea floor between 25 m and 65 m was rocky substrate (Davis et al., 1998;

Cortes Bank				San Clemente Island			
Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population	Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population
12.3 ±8.8	2.6	232	2853.6 ±2041.6	3.1 ±2.8	0.8	392	1215.2 ±1097.6
6.1 ±2.8	1.5	423	2580.3 ± 1184.4	2.6 ±1.8	2.4	278	722.8 ±500.4
4.0 ±2.7	0.7	483	1932 ±2114.1	0	0.7	219	0
8.0 ±3.1	4.8	1138	7365.9 ±5340.1	1.5 ±0.2	3.9	889	1938 ±1598

Hobday and Tegner, 2000; Hobday et al., 2001). Using this assumption, the total amount of white abalone habitat in southern California was estimated to be only 752 ha (Davis et al., 1998; Hobday et al., 2001). The results of surveys from the present study at only three sites (Tanner and Cortes Banks and San Clemente Island) revealed 3646 ha of rocky substrate between 30 and 60 m, which is much higher than estimates based on the 3% rocky habitat assumption. Thus, the total available habitat area for white abalone and other benthic dwelling organisms in southern California is likely far greater than previously reported.

The definition of available white abalone habitat, however, may need further refinement if white abalone exhibit a preference for a certain type of rocky substrate. Cochrane et al. (2005) suggested that white abalone prefer the edges of reefs at the sand-rock interface rather than the areas in the middle of the reef. Although there is some qualitative evidence supporting this idea, there have been no conclusive studies on specific habitat preferences. The only conclusion that can be drawn in relation to habitat preference from the present study is that white abalone are not typically found in areas with no rock (i.e., sand only). Even if white abalone were found only at the sand-rock interface, our estimates of available habitat would still far exceed past estimates. Although the time and effort involved in mapping habitat may lead to the temptation to make broad generalizations to estimate habitat types and amounts, the results of this study have shown that specific habitat mapping is necessary to accurately identify the amounts of each type of habitat existing in a particular area.

The depth distribution of white abalone at these three sites was grouped into three depth bins (30–40 m, 40–50 m, and 50–60 m) and was less stratified than predicted according to preliminary surveys at Tanner Bank. The number of abalone was highest in the middle depth bin (40–50 m) at Tanner Bank during 2002 and 2004, but only significantly so in 2002. The highest number of abalone observed at Cortes Bank was in the shallowest depth bin (30–40 m). Too few abalone were sighted at San Clemente Island and they were not included in the analysis. These results indicate that there are not clear, broad trends in depth distribution that can be applied to all sites, although the deepest depth bin did yield the fewest abalone sightings at all sites. It is also possible that the only realistic trends observed were those at Tanner Bank in 2002 because of the relatively large number of animals observed at this site.

The white abalone population in California has been estimated to number less than 3000 (Davis et al., 1998; Hobday and Tegner, 2000; Hobday et al., 2001). In this study a total of between 15,187 and 22,123 white abalone was estimated at two offshore banks and one island location. Our population estimate is greater for two reasons: 1) the multibeam sonar maps revealed more habitat than was previously known to exist, and 2) search effort, and therefore the calculation of density, was dependent on suitable habitat, i.e., densities were not artificially deflated by including portions of surveys conducted in inappropriate habitat (e.g., sand).

The highest densities (19.8 abalone/ha between 40 and 50 m) were observed at Tanner Bank in 2002. Previous surveys at Tanner Bank underestimated habitat area and included the entire search area without regard to depth or habitat to determine density. A re-examination of data from surveys conducted by the Delta submersible in 1999 at Tanner Bank (Haaker et al.[2]) yielded an overall density of 15.7 abalone/ha. This value varies only slightly from our overall density esti-

mate of 13.0 abalone/ha. Densities were lower overall in our surveys conducted at Tanner Bank in 2004, and the most significant differences were apparent in the 40–50 m depth range. These lower densities in surveys conducted only two years after initial surveys are noteworthy and worrisome, especially because Tanner Bank is a site where the population was thought to be relatively stable.

The density of white abalone prior to commercial and recreational exploitation is poorly known, and the few reported estimates are the subject of considerable speculation. Tutschulte (1976) reported an estimate of white abalone density of 2300 abalone/ha, based on three 10-m^2 quadrats. Because of the small sample size and lack of replicate sites, caution should be used when applying this estimate to all of California. However, it is important to note that one cluster of five white abalone was observed in the present study, which would lead to a local density close to that reported by Tutschulte (1976). It is also of interest to note that Shepherd et al. (2001) suggested that once populations of *Haliotis laevigata* reached densities below 0.25 abalone/m^2 (2500 abalone/ha) management action should be taken, and therefore estimates of 0.23 abalone/m^2 reported by Tutschulte (1976) were not extremely high.

More recently Rogers-Bennett et al. (2002) used historical landings data and the habitat area estimated by Davis et al. (1998) and Hobday et al. (2001) in an attempt to reconstruct past population densities. Applying the 3% rocky habitat criteria referred to above (Discussion section, paragraph 1) (Thompson et al., 1993), Rogers-Bennett et al. (2002) calculated a density of 479 abalone/ha for all of California and a density of 1623 abalone/ha for San Clemente Island, where 75% of the landings were reported. These densities are lower than those reported by Tutschulte (2300 abalone/ha; 1976), but the more recent estimate is also too high because the proportion of rocky habitat is greater than 3%, as observed in the present study. The maximum density observed in the present study (19.8 abalone/ha) is only an order of magnitude less than Rogers-Bennett et al.'s (2002) calculation of historic density for all of California (479 abalone/ha), but is two orders of magnitude less than the estimates by Tutschulte (2300 abalone/ha, 1976). Regardless of the problem of inflated density estimates, the densities observed in the present study at San Clemente Island were less than 5 abalone/ha at all depths, which is astoundingly lower than the 1623 abalone/ha calculated by Rogers-Bennett et al. (2002).

Whether the existing white abalone populations are viewed as viable depends largely on the validity of estimates of past population distributions and densities and on establishing confidence in current density estimates. Total abundance of individuals becomes irrelevant if these animals are distributed such that densities within a particular area are below the critical level necessary for successful reproduction. The relatively deep range of *H. sorenseni* is outside the range of dense macroalgal growth, and therefore we can assume that the ROV does an adequate job in identifying animals within its field of view (2 m). Based on the assumption that we are actually sighting nearly all of the animals that are within the search range, our data indicate that the majority of individuals at these sites are greater than 5 m (linear distance) from any other individuals along and between transects, and that many are over 30 m away from a potential mate. These distances well exceed what has been shown to be a critical minimum distance (≤2 m) for successful spawning and fertilization in other species of abalone (e.g., *Haliotis laevigata*; Shepherd and Brown, 1993; Babcock and Keesing, 1999; Shepherd et al., 2001). The large distances between individuals coupled with density estimates that are several orders of magnitude lower than those necessary for a viable population (Shepherd et al., 2001) would indicate that white abalone populations are currently in a dire state.

Despite generally large distances between individuals, an analysis of dispersion within the population surveyed at Tanner Bank in 2002 showed a large proportion of individual sightings within 30 m of another sighting. Additionally, there was a high degree of contagion between individuals in 250-m^2 subsamples at depths of 40–50 m. It may be true that white abalone at this site are aggregated on a larger scale, indicating that certain habitats within their most prevalent depth range (40–50 m) may promote higher survival of white abalone. However, ultimately, if animals are not packed densely enough at smaller scales, successful spawning and fertilization will not occur. This study highlights the importance of establishing accurate density estimates at appropriate scales for guiding assessments of population viability and future enhancement protocols.

The mean sizes of white abalone observed in the present study varied little between sites and were comparable to those observed during 1999 submersible surveys at Tanner Bank and Cortes Bank (Behrens and Lafferty, 2005). The size distribution of white abalone did differ slightly between the two banks and island location. More notable was an apparent shift in the size distributions of animals observed at Tanner Bank in 2002 versus those observed in 2004. Unlike in 2002, there were no large individuals observed in 2004, indicating a possible die-off of older individuals and a lack of new, younger individuals to fill this size class. No white abalone smaller than 9.0 cm (approximately three years old; Tutschulte, 1976) were observed at any of the sites. If this were a self-sustaining population, smaller individuals indicating recruitment from several preceding year classes would be present, although the likelihood of sighting abalone recruits and juveniles younger than three years is not very high. Juvenile white abalone shells are mottled red in color and settlement occurs on pink crustose coraline algae-covered rocks, thus making them very cryptic during the first few years of life. Even during historic periods when white abalone density was much higher than cur-

rent levels, juveniles were observed on extremely rare occasions (Owen[4]). Thus, the absence of small individuals during ROV observations does not rule out recent recruitment to this population. Consequently, although recruitment in the last three years may be undetectable, recruitment from the last three decades should be evident in our surveys.

Conclusions

The use of detailed sonar mapping techniques has proven to be an invaluable method to estimate amounts of different habitat types for the purposes of quantifying marine organisms within their specific habitat. Specifically, white abalone restoration efforts would be greatly enhanced by more surveys incorporating high-resolution bathymetric maps that would serve to better define the characteristics of suitable white abalone habitat. Our concept of what a viable white abalone population is would benefit from more accurate density estimates for other areas within the historic range and from a better understanding of how white abalone are distributed within populations.

The ultimate goals of recovery and eventual removal of white abalone from the Endangered Species List depends upon establishing confidence in the demographic parameters that define a viable white abalone population. It has become apparent that conducting studies such as this one, with continuing efforts to improve sample standardization techniques over time, is critical to achieving recovery goals.

Acknowledgments

Multibeam sonar mapping during the 2002 cruise was funded by the National Fish and Wildlife Foundation through a grant to the California Department of Fish and Game. Dan Richards provided data from the 1999 Channel Islands National Park white abalone survey. John Wagner, Anthony Cossio, Ben Maurer, Scott Mau, and David Murfin piloted the ROV and provided technical support. The officers and crew of the RV *David Starr Jordan* ran transects and survey lines. Chuck Oliver participated in cruises and, along with Nancy Lo, designed the microhabitiat analyses. Pat Iampietro, Carrie Bretz, Kate Thomas, Jason Mansour, Tiffany Van, Andrew Rapp, Bryan Jones, Josh Sampey, and Saori Zurita helped with multibeam sonar data acquisition, processing, and analysis. David Murfin, Lara Asato, and several anonymous reviewers provided comments that improved earlier versions of this manuscript.

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Experiments in gear configuration to reduce bycatch in an estuarine squid-trawl fishery

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Abstract—Three experiments were performed in an estuarine squid-trawl fishery in New South Wales, Australia, to test modifications to trawl nets. Lateral mesh openings were experimentally increased and physical bycatch reduction devices (BRDs) were placed in codends. These modifications aimed to reduce nontargeted catches of fish, while maintaining catches of the targeted broad squid (*Photololigo etheridgei*) and bottle squid (*Loliolus noctiluca*). Compared to conventional codends made with 41-mm diamond mesh, codends made with different posterior circumferences and larger 45-mm mesh had no significant effect on the catches of any species. The best performing configurations involved the installation of BRDs designed to separate organisms according to differences in behavior. In particular, versions of a composite square-mesh panel reduced the total weight of bycatch by up to 71% and there was no significant effect on the catches of squid. The results are discussed in terms of the probable differences in behavior between fish and squid in codends. After this study, a square-mesh panel BRD was voluntarily adopted throughout the fishery.

Manuscript submitted 26 April 2005 to the Scientific Editor's Office.

Manuscript approved for publication 6 December 2005 by the Scientific Editor.

Fish. Bull. 104:533–541 (2006).

The incidental catch of nontarget organisms (termed "bycatch") by commercial fishing gears will remain an important issue in the management of fisheries. Article 7.6.9 of the Food and Agriculture Organization's Code of Conduct for Responsible Fisheries (FAO, 1995) notes "States should take appropriate measures to minimize waste, discards, catch by lost or abandoned gear, catch of non-target species, both fish and non-fish species, and negative impacts on associated or dependent species, in particular endangered species." Several options are available for achieving these aims (Hall, 1996), but the most common strategy involves technological improvements to fishing gears that reduce unwanted mortality due to fishing (Kennelly and Broadhurst, 2002).

Much research into gear design to reduce bycatch has been undertaken in demersal trawl fisheries and especially those targeting shrimp (for reviews see Kennelly, 1995; Broadhurst, 2000). This research reflects the seriousness of bycatch issues in these fisheries and, in particular, the incidental mortality of key species such as marine turtles and juveniles of commercially and recreationally important fish. Considerably less work has been done on bycatch in other fisheries, including those targeting cephalopods.

The global catch of squid has been estimated at 2.8 million tonnes (t) per year (FAO[1]). Squid are harvested with highly-selective jigs or less selective gill nets, seines and, more commonly, trawls (Rathjen, 1991; Morais da Cunha and Moreno, 1994; Simón et al., 1996). Large-scale use of pelagic gill or drift nets has been restricted because of concern about incidental catches (e.g., Burke et al., 1994; Piatt and Gould, 1994). Despite their widespread use, very little work has been done to modify towed gears so that they selectively harvest squid. In one of the few studies relevant to this issue, Glass et al. (1999) attached video cameras to the anterior sections of trawls targeting longfin squid (*Loligo pealeii*) in the Atlantic Ocean and observed that squid positioned themselves considerably higher in the trawl than fish. It was suggested that this difference in behavior could be used to separate catches.

[1] Food and Agriculture Organization (FAO). 2005. FAO Fisheries Global Information System. www.fao.org/fi/figis [accessed on 23 Nov 2005]. Average annual global production of all squid species for 2000 to 2003.

In New South Wales (NSW) Australia, arrow squid (*Nototodarus gouldi*), mitre squid (*Photololigo* sp.) and southern calamari (*Sepioteuthis australis*) are important in the legally retained bycatch from fish and prawn trawlers working in oceanic waters. In addition, two species of squid are specifically targeted by up to 20 trawlers with modified, single-rigged prawn trawls in Broken Bay (Fig. 1). Broad squid (*P. etheridgei*) (typically 30–290 mm mantle length [ML] when harvested) represent the majority of the total catch (approximately 25–50 t per year since 1997), although the smaller bottle squid (*Loliolus noctiluca*) (30–90 mm ML when harvested) are also retained and sold, primarily as bait for recreational anglers. Additional details on the local biology of *P. etheridgei* can be found in O'Donnell (2004).

The designs of trawls used to catch these squid vary among operators, but all are restricted by lengths of the headline (<11 m) and sweeps (<5 m) and minimal and maximal mesh openings of 40–60 mm in the body and 40–45 mm in the codend. To maximize catches of the smaller bottle squid, all operators use codends of the minimal legal mesh size of 40 mm, with anterior sections of 100 meshes in circumference attached to posterior sections of at least 150 meshes in circumference (made with thick twine), which are designed to reduce lateral-mesh openings (Broadhurst and Kennelly, 1996).

The configuration of conventional codends in the Broken Bay squid-trawl fishery means that these trawls are poorly selective and therefore, in addition to the targeted squid, they also retain large quantities of bycatch. Preliminary data from a 3-year observer-based study of catches in the early 1990s (DPI[2]) indicated a bycatch-to-squid ratio of up to 4:1 (by weight). Although a subset of this bycatch includes some species that the fishermen are legally permitted to retain, most of the bycatch is small, unwanted fish, including juveniles of several commercially and recreationally important species. Concerns over the mortality of these individuals and the negative impacts on stocks led us to test the utility of modifications to fish- and prawn-trawl codends for improving selection of species in squid trawls. Such experimental work has not previously been completed in squid-trawling fisheries.

A series of explicit hypotheses were tested in the fishery. It was proposed that devices designed to reduce bycatch would 1) cause differential changes in catches, by reducing bycatch but causing no important reduction in catches of squid; 2A) not cause disproportionate bycatch of small or large fish (i.e., would not influence the distributions of sizes of fish caught); 2B) not cause differential effects, so that subsequent incidental catches had similar mixtures of types and relative abundances of fish species as before; and, 2C) not cause relatively larger catches of particular fish species, nor of juveniles of commercial species.

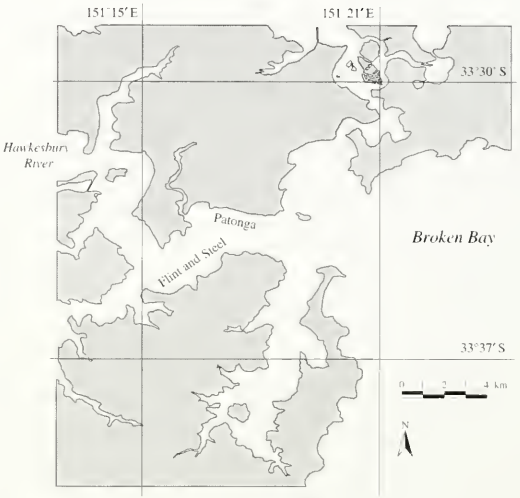

Figure 1

Location of Broken Bay and the two areas trawled (Patonga, and Flint and Steel). Broken Bay is 35 km north of Sydney, New South Wales, Australia.

Materials and methods

This research was completed on two commercial squid-trawl grounds in Broken Bay NSW (Fig. 1) between February and September 2002 by using a chartered squid trawler (9.2 m in length). The vessel was rigged with a single, conventional 4-seam otter trawl made from 60-mm (all mesh sizes refer to stretched opening) polyethylene (PE) netting (headline of 11 m; Fig. 2) towed between 0.8 and 1.8 m/s over a sandy substratum at depths ranging from 5 to 15 m. A zipper (Buraschi S146R, Milan, Italy, 1.5 m in length) was attached at the posterior body of the trawl to facilitate changing codends (Fig. 2).

Codends and BRDs examined

Five codends of different design were made from dark PE netting with total lengths and anterior fishing circumferences (i.e., the expected circumference of the codend during towing—[Broadhurst et al., 1999]) of 2.4 and 1.5 m, respectively (Fig. 3, A–E). All codends had zippers (Buraschi S146R, 1.5 m in length) attached at their anterior ends. Four of the codends were made within existing regulations and had anterior sections made from 40-mm knotted netting (2-mm diameter-ø twisted twine) with a length and circumference of 35

[2] DPI (New South Wales Department of Primary Industries). Unpubl. data. 1992. [Data are on file at New South Wales Department of Primary Industries, PO Box 21, Cronulla, 2230, NSW, Australia.]

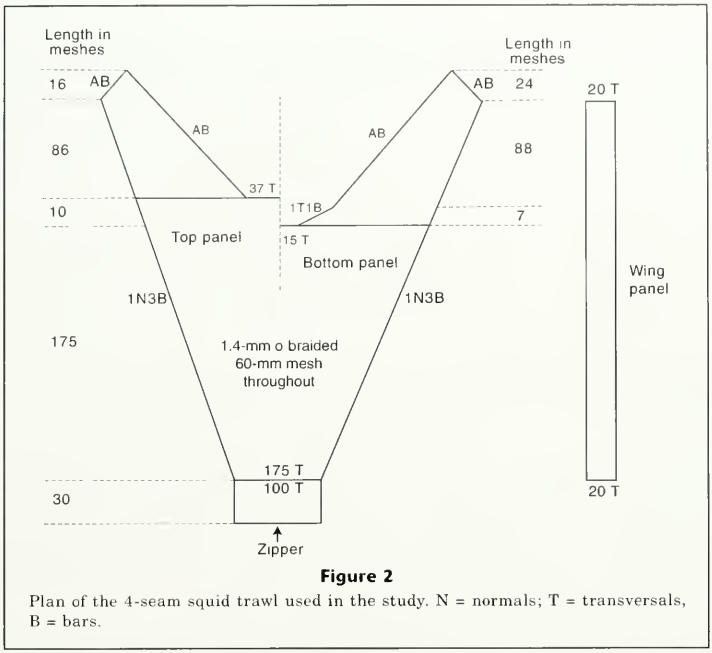

Figure 2

Plan of the 4-seam squid trawl used in the study. N = normals; T = transversals, B = bars.

and 100 meshes, respectively, and posterior sections with a length of approximately 1 m, but different mesh circumferences and sizes (all meshes were made from 3-mm ø braided twine; Fig. 3, A–D). The first codend (41/150) represented commercially used designs with a posterior section of 41-mm mesh and a circumference of 150 meshes (Fig. 3A). The second codend (41/100) had a posterior section made from the same mesh, with a circumference of 100 meshes (Fig. 3B). The third and fourth designs (45/150 and 45/100, respectively) had posterior sections with the same circumferences as those above, but were made from 45-mm mesh (Fig. 3, C and D). The fifth codend design (termed the "square-mesh codend") was made entirely of 30-mm mesh (1.4-mm ø twisted twine) hung from the bar (i.e., the meshes were oriented so that they were square shaped) and had a total length and fishing circumference of 144 and 90 bars, respectively (Fig. 3E).

Four variations of behavioral-type bycatch reduction devices (BRDs) were tested in combination with certain codends (Fig. 3, F–I). All BRDs were installed in the top anterior section of the relevant codend at a distance starting 1.1 m anterior to the last row of meshes in the posterior section according to the specifications provided by Broadhurst et al. (2002). The first BRD (the diamond BRD; see Broadhurst et al. [2004]) was a diamond-shaped opening (11 × 11 bars) cut into a conventional 41/150 codend (Fig. 3F). The second and third BRDs were composite square-mesh panels (CSMP; Broadhurst and Kennelly[1996]) with 90- or 75-mm mesh, respectively, hung from the bar in the main escape panels and were inserted into the conventional 41/150 and 41/100 codends. These modified codends were called the "90-CSMP" and "75-CSMP" codends (Fig. 3, G and H). The fourth BRD was inserted into the square-mesh codend (termed the "75-panel codend"; Fig. 3I); it was a simple panel of 75-mm mesh hung from the bar (and having the same dimensions as that used in the CSMP codend).

Experimental procedure

Three independent experiments were completed during 2002 to identify an appropriate combination of codend and BRD that minimised bycatch whilst maintaining catches of squid. Experiment 1 (25 February–1 March 2002, five days, two replicate hauls/day) tested predictions about the effect of 1) changing the posterior codend circumference within the maximal and minimal codend mesh sizes legally permitted in the fishery; and 2) using the diamond and CSMP BRDs located in the commercially used 41/150 codend. Experiment 2 (29 July–9 August 2002, 10 days, two replicate hauls/day) repeated experiment 1 above (but with additional replication to increase the power to differentiate between the codends) and also tested the effectiveness of the square-

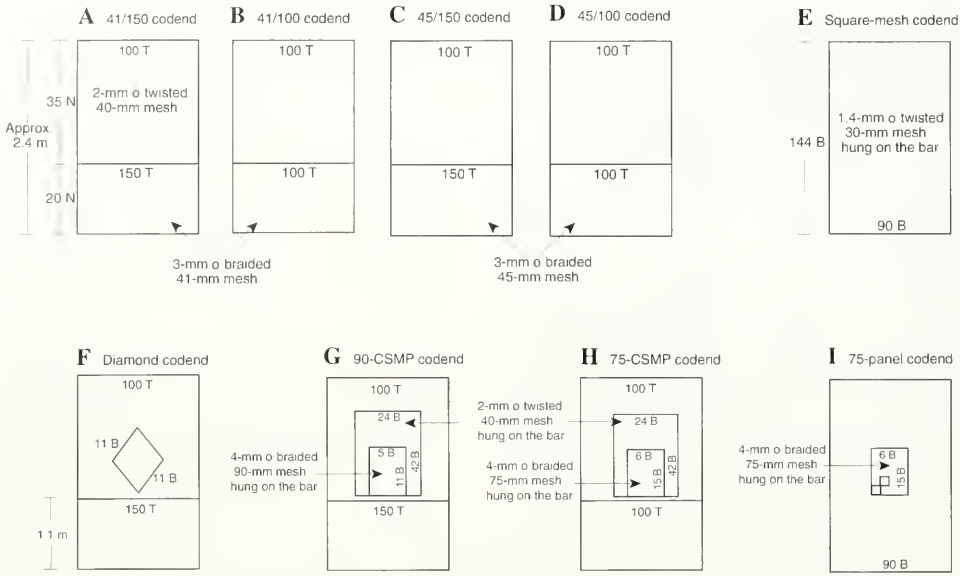

Figure 3

Schematic representation of the codends and bycatch reduction devices tested during the experiments. The 41/150 codend is the conventional design used in the fishery. N = normals; T = transversals, B = bars.

mesh codend. Experiment 3 (26 August–6 September 2002, 10 days, three replicate hauls/day) compared the 41/100 and square-mesh codends (the most appropriate non-BRD codends; see Results section), with and without their respective 75-CSMP and 75-panel BRDs installed.

In each experiment, the daily position and order of the codends being tested were determined randomly and they were alternately used in normal commercial hauls of 30-min duration between 0700 and 1500 hours. Depending on the number of codends being tested, we attempted two or three balanced replicates of each treatment on each day. Haul location was determined by the skipper and varied between the two squid trawl grounds in Broken Bay (Fig. 1) according to the presence of jellyfish, *Catostylus* sp., which reduced the efficiency of the trawl. Data collected from each replicate haul included the numbers and weights of all taxa and the sizes of commercially and recreationally important species. When large numbers (several hundred) of any species were caught, a randomly selected subsample (approximately 25–50% of the total) was measured. Fish were measured to the nearest 0.5 cm fork length; carapace lengths of crustaceans were measured to the nearest 0.1 cm.

Results

Bycatch and target squid

The primary hypothesis for this study was that the devices designed to reduce bycatch would cause changes in catches, by reducing bycatch but causing no important reduction in the catches of squid. This hypothesis was tested by using univariate statistical methods applied to the results from all three experiments. In Experiment 1, the diamond and 90-CSMP codends caught less bycatch (about 74% less on average) than the other types of gear (Table 1). About 50% of the bycatch were discards, including teleost fish such as tailor (*Pomatonus saltatrix*) and mulloway (*Argyrosomus japonicus*). There were, however, no significant reductions in catches of squid, although catches were smaller with the diamond codend. As a result, later experiments were mostly done with larger mesh sizes. There were no effects of altering other components of the gear (circumference or meshsize of the codend). Catches of squid were significantly different on the two days (Table 1A), but there was no interaction with the type of codend; therefore differences among types of gear were consistent. Sources of variation that were determined to be nonsignificant at $P>0.25$

Table 1

Analyses of catches using six types of gear from experiment 1 during February–March 2002. Data are weights of catches from Flint and Steel, fished for 2 different days (a random factor). Codend (a fixed factor) is the comparison of 41/150, 41/100, 45/150, 45/100, diamond and 90-CSMP (composite square-mesh panel) codends. $n = 2$ replicate hauls for each treatment on each day.

A Analyses of variance

			Bycatch			Squid		
Source of variation		df	Mean square	*F*	*P*	Mean square	*F*	*P*
Codend	= *C*	5	1.51	3.16[a]	<0.04	0.24	0.63[a]	>0.65
Day = *D*	= *D*	1	0.46	0.96[a]	>0.30	2.50	6.51[a]	<0.05
C × *D*		5	0.39[p]			0.33[p]		
Residual		12	0.51[p]			0.40[p]		
[p]Pooled residual		17	0.48			0.38		

B Mean untransformed weight (kg, [±standard error, $n=4$]) of bycatch and squid per haul and Student-Newman-Keuls tests; "<" indicates significant differences at $P<0.05$; "=" indicates $P>0.05$.

	Codend											
	Diamond		90-CSMP		41/100		41/150		45/100		45/150	
Bycatch	7.7 (2.3)	=	6.4 (1.7)	<	23.1 (6.1)	=	22.3 (2.2)	=	24.8 (6.9)	=	17.3 (7.0)	
Squid	2.2 (0.6)	=	3.5 (0.8)	=	2.9 (0.7)	=	3.9 (1.2)	=	3.2 (1.2)	=	4.3 (1.2)	

were pooled and catches were transformed to natural logarithms to stabilize variances (Underwood, 1997).

A second analysis compared the diamond and 90-CSMP with the conventional 41/50 codend in two areas (in estuarine waters off Patonga, and Flint and Steel, see Fig. 1), to check consistency across fishing-grounds. A balanced set of replicated hauls with each type of gear was obtained. Again, the two BRDs caused large and significant reductions in bycatch compared with the conventional net. Although catches of squid were smaller, they were not significantly so and there was a large reduction in the ratio of weight of bycatch to weight of squid caught. Strikingly, although there was considerable variation from day to day and between locations in the amount of bycatch, there were no interactions with experimental gear used. Therefore, reductions in bycatch were consistent under the different conditions that are typical to the fishery.

Experiment 2 compared catches with the four codends without BRDs, as in experiment 1, with catches with the square-mesh codend. There were complex differences in the amount of bycatch caught with different types of gear, despite many catches being smaller than those in experiment 1. More bycatch was caught with the 45/150 codend than with the 41/150 codend (i.e., an effect of mesh size). This difference was, however, detected only for the 150 codend. There was also an effect of circumference of the codends (41/100 caught more bycatch than did 41/150), but only for the commercial (41-mm mesh) codend. This finding explains the significant interaction between mesh-size and circumference in the analysis in Table 2.

Again, although there were differences in amounts of bycatch, there were no significant or detected differences in catches of squid (Table 2, A and B); therefore it was possible to achieve reductions in bycatch without any notable effect on the commercial catch.

During experiment 3 catches were generally small and patchy. Data were very variable, but it was possible to complete five days of trawling with the 41/100 and square-mesh codends with or without their square-mesh BRDs. There was a very marked reduction in bycatch when a BRD was added to a codend, regardless of whether there was a square-mesh panel in the codend or not (Table 3A). Again, there were no influences on the catches of squid, but the ratio of weight of bycatch to weight of squid was smaller for both types of mesh when a BRD was added (analysis of ratios in Table 3B).

Sizes of species in bycatch

The secondary hypotheses of this study, that devices to reduce bycatch would 2A) not cause disproportionate bycatch of small or large fish; 2B) not cause differential effects; and, 2C) not cause relatively larger catches of particular species, were tested with multivariate statistical methods.

Analyses of sizes of bycatch were uniform in their outcome—there was no measurable difference on the size composition of species caught for any of the devices tested. As examples, two species of fish were present in

Table 2

Analyses of catches from experiment 2 during July–August 2002. Data are weights of catches from two locations (Patonga, Flint and Steel; a random factor), each sampled over four different days (randomly, nested in location). Square-mesh panels were compared with the 41/150, 41/100, 45/150, 45/100 codends. There were $n = 2$ replicate hauls of each gear on each day in each location.

A Analyses of variance

			Bycatch			Squid		
Source of variation		df	Mean square	*F*	*P*	Mean square	*F*	*P*
Treatment	$= T$	4	1.61			0.55		
Square-mesh vs. others	$= S$	1	0.55	0.87	>0.35	0.72	1.3	>0.20
Mesh: 41 vs. 45	$= M$	1	1.14	1.80	>0.15	0.47	0.8	>0.35
Circumference: 100 vs. 150	$= C$	1	2.40	3.80	<0.05	0.30	0.5	>0.45
$M \times C$		1	2.40	3.70	<0.05	0.57	0.71	>0.20
Location	$= L$	1	2.17			1.13		
$T \times L$		4	0.80[P]			0.19[P]		
Days (L)	$= D(L)$	6	4.9	7.10	<0.001	0.69	1.2	>0.25
$T \times D$		24	0.72[P]			0.62[P]		
Residual		40	0.56[P]			0.50[P]		
[P]Pooled residual		68	0.63			0.56		

B Mean weight (kg, (±standard error, n=16)) of bycatch and catch in various treatments

		Circumference (no. of meshes)			
		100	150	100	150
Mesh	41-mmm	56.8 (17.5)	28.1 (5.4)	14.6 (2.1)	11.6 (1.8)
	45-mm	44.6 (6.7)	60.0 (12.9)	13.2 (1.5)	13.9 (1.7)
	Square-mesh (30 mm)	48.7 (10.5)		15.2 (1.9)	

most hauls, were fairly abundant in bycatch, and were each represented by a range of sizes. Tailor (*Pomatomus saltatrix*) were grouped into five length classes with approximately equal numbers of fish in each class (140–145, 146–170, 171–195, 196–220, 221–280 mm); the snapper *Pagrus auratus* were also so grouped into five length classes (70–105, 106–120, 121–135, 136–155, 156–230 mm). Data were analyzed as the proportion of fish in each size class, to remove differences due to different numbers of fish caught in the various types of gear. Size classes were then used as variables in multivariate analyses to compare the various types of gear.

Using data from experiment 1, we detected no differences among types of gear in the proportional size frequencies of either tailor or snapper. The mean Bray-Curtis dissimilarities between pairs of samples were all very similar to the mean measures within samples (i.e., among replicates); therefore there was no suggestion of differences in size frequencies among types of gear for these species. Multidimensional scaling plots (not included, Clark and Gorley[3]) supported this result because the centroids of the size classes of both species were not clustered by type of gear.

Composition of bycatch

The types of species and relative abundances of species in the bycatch were analyzed from several times of sampling. Analyses used data without squid because numbers of squid are irrelevant to the bycatch. Typically, there were no detected differences in assemblages of species in the bycatch. One exception, in Experiment 2 is described. In our study, analyses of Bray-Curtis dissimilarities showed some differences among types of gear, where the square-mesh codend caught a different assemblage. It seemed that fewer whitebait (*Hyperlophus vittatus*) were being caught when the square mesh was used (this was confirmed by SIMPER[4] analysis, which showed that numbers of whitebait were an important variable for discriminating between samples). To test the validity of this conclusion, we performed analyses, omitting numbers of whitebait. This time, all differences

[3] Clarke, K. R., and R. N. Gorley. 2001. Primer version 5: user manual/tutorial, 91 p. Primer-E Ltd, Plymouth, U.K.

[4] See footnote 3.

Table 3

Analyses of catches from four codends (41/100, square-mesh, 75-panel, 75-CSMP [composite square-mesh panel]) from experiment 3 at Flint and Steel during August–September 2002. Data are weights of catches on five days, during each of which there were $n = 3$ independent hauls with each type of gear.

A Analysis of variance

			Bycatch			Squid			Ratio: bycatch/squid		
		df	Mean square	F	P	Mean square	F	P	Mean square	F	P
Mesh: 41 vs. square mesh	$= M$	1	0.9	1.4	>0.25	0.001	0	>0.95	0.3	0.8	>0.35
+BRD vs. –BRD	$= B$	1	4.5	6.6	<0.01	0.1	0.2	>0.60	2.4	3.1	>0.15
$M \times B$		1	2.5	3.6	>0.05	0.2	0.4	>0.50	1.0	0.4	
Days	$= D$	4	5.7	8.4	<0.001	0.7	0.7	>0.60	2.5	6.0	<0.001
$M \times D$		4	0.8[p]			0.5[p]			0.2[p]	0.4	>0.50
$B \times D$		4	0.8[p]			0.6[p]			0.8	1.8	>0.15
$M \times B \times D$		4	0.6[p]			0.4[p]			0.2[p]		
Residual		40	0.7[p]			0.6[p]			0.5[p]		
[p]Pooled residual		52	0.7			0.6			0.41	(48 df)	

B Multiple comparisons: mean weight (kg, (±standard error, n=30)) of bycatch, squid, and ratio of bycatch/squid; * indicates a difference (Student-Newman-Keuls test; P<0.05).

Bycatch		Squid		Ratio: bycatch/squid	
–BRD	+BRD	–BRD	+BRD	–BRD	+BRD
3.3 (0.5)	2.6 (0.4)*	1.6 (0.2)	1.6 (0.2)	6.0 (3.8)*	1.6 (0.4)

among types of gear disappeared. Whitebait are not an important concern for management in this fishery and results like these were not obtained in the other experiments; therefore no further consideration was given to this matter. Results from this study indicate that the composition of assemblages of bycatch was not altered by combinations of experimental gear and there were no detectable influences on particular species.

These multivariate results indicated that, with the exception of whitebait, none of the secondary hypotheses (2A, 2B, or 2C) could be rejected. These experiments did, however, have limited power to detected small effects because of the large variability of the catches and the relatively limited replication completed.

Discussion

The results demonstrated that the general concepts used to improve species selection in fish and shrimp trawls have similar application for squid. Nevertheless, the specific designs of modifications require careful consideration, according to several fishery-related factors. One of the starting points for reducing bycatch in all towed gears involves examining simple changes to the size and shape of mesh in the codend, because this is where most of the selection is believed to occur (Wileman et al., 1996). Broadhurst and Kennelly (1996) and Broadhurst et al. (2004) showed that codends made from thick twine and with large posterior circumferences, like those used conventionally by squid trawlers in Broken Bay, have very narrow lateral mesh openings and have poor selectivity. Three of the simplest methods for improving selection in codends involve 1) reducing the posterior circumference (e.g., Broadhurst and Kennelly [1996]), 2) increasing the mesh size (e.g., Reeves et al. [1992]), or 3) orienting meshes, typically orienting 60–90% of the size of the existing diamond-shaped mesh on the bar so that they are square shaped (e.g., Thorsteinsson [1992]; Broadhurst et al. [2004]).

These three modifications were tested during the present study but, with the exception of the square-mesh codend, none were demonstrated to significantly improve species selection or influence the sizes of individuals caught. The considerable temporal variability in catches and a concomitant lack of power to detect small effects may partially account for the lack of differences detected, but a more likely explanation is that the magnitude of changes to mesh openings in relation to the sizes of target and bycatch species was insufficient. Given that some small fish escaped from the square-mesh codend, future work would probably benefit from further examination of increasing codend mesh openings as a means for reducing bycatch.

In contrast to subtle modifications to codend meshes that were tested, it was demonstrated that BRDs

designed from an understanding of the behavior of fish and squid were effective in allowing fish to escape and did not significantly reduce the catches of squid. The escape of fish through these BRDs was a direct consequence of 1) their behavior and species-specific swimming abilities in the trawl (Wardle, 1983; Watson, 1989) and 2) the location of the BRDs with respect to the influences of water-flow (Broadhurst et al., 2002). More specifically, when fish enter the codend they are often herded together and herding invariably initiates movement towards the top and sides. The density of the school and any species-specific behavioral responses (Watson, 1989) determine the extent of such movement. Panels of square-shaped mesh, if strategically positioned, have been demonstrated to allow actively swimming fish to escape the trawl through the large openings in the square-shaped mesh (Broadhurst, 2000). An important contributing factor is the effect of anteriorly displaced water in front of the catch, which reduces relative flow and assists small fish to maintain their position in the codend. Broadhurst et al. (2002) demonstrated that these effects diminish with increasing distance forward and that the optimal location for BRDs designed on fish behavior is up to 1.2 m anterior to the last row of meshes in the posterior section of the codend (i.e., the position of all BRDs examined in our study).

The behavior of squid in trawls, codends, or near BRDs has not been examined in detail. Glass et al. (1999), however, observed that the reaction of schooling *L. pealeii* during initial detection of the gear was similar to fish. Individuals orientated away and then, as a result of compensatory movements in response to shifts in their visual field (termed the optomotor response), attempted to maintain position in the mouth and body of the net. After a short period, all squid were observed to stop swimming, turn, rise in the net, and fall back toward the posterior section of the trawl and toward the codend. Their behavior in this region of the net was not documented, but, given the lack of significant reductions in the catches of squid (or other cephalopods) by prawn trawls containing behaviour-based BRDs (e.g., Broadhurst et al. 2002) and the results observed in our study, active escape is probably limited.

There was a nonsignificant reduction in the weight of squid from the codends containing BRDs in experiment 1, and especially the diamond BRD, but this reduction probably occurred during retrieval of the codend. Typically, once the trawl is winched to the surface, a delay of up to three minutes can occur while the vessel is stopped, the retrieval line is connected, and the codend is brought onboard. During this period, any squid in the anterior codend or extension section may wash forward and out of the escape opening in the BRD. Watson (1989) observed similar effects during the retrieval of prawn trawls in the Gulf of Mexico and, more recently, Brewer et al. (1998) highlighted this escape route as being a major cause of loss of prawns from several BRDs in trawls used in the Gulf of Carpentaria, Australia. A simple way of minimizing the potential for such losses when using the diamond BRD would be to keep the vessel moving, thus maintaining drag on the codend, during retrieval. A simpler and more practical solution would be to substitute the square-mesh BRD with panels made from 75-mm mesh hung on the bar, since the 75-CSMP and 75-panel codends tested in Experiment 3 showed no evidence of loss of squids. Assuming that fish escaping from the CSMP survive the process (Broadhurst et al., 1997), the results presented in this study support the adoption of the CSMP codend in Broken Bay squid trawls. As a consequence of this study, and the co-operative relationship established between the NSW Department of Primary Industries and commercial fishermen, a square-mesh panel BRD has been voluntarily adopted throughout the Hawkesbury River squid-trawl fishery.

Acknowledgments

This study was funded by the Australian Research Council Linkage Scheme (Project C00106975) and the NSW Department of Primary Industries. The work would not have been possible without the technical expertise and support of Broken Bay squid fishermen Mark Peterson, Carl Blacklidge, Graeme Hillyard, Chris Stapleton, and Rolf Norington. We thank Bob Hunt, Katie O'Donnell, Simon Gartenstein, Andres Grigaliunas, Craig Myers, Sophie Diller, and David Blockley for their technical assistance. Steve Kennelly developed the original proposal for this study and suggested valuable improvements to the manuscript. Constructive comments from two anonymous reviewers were also greatly appreciated.

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The relationships between fish assemblages and the amount of bottom horizontal beam exposed at California oil platforms: fish habitat preferences at man-made platforms and (by inference) at natural reefs

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Abstract—Between 1995 and 2002, we surveyed fish assemblages at seven oil platforms off southern and central California using the manned research submersible *Delta*. At each platform, there is a large horizontal beam situated at or near the sea floor. In some instances, shells and sediment have buried this beam and in other instances it is partially or completely exposed. We found that fish species responded in various ways to the amount of exposure of the beam. A few species, such as blackeye goby (*Rhinogobiops nicholsii*), greenstriped rockfish (*Sebastes elongatus*), and pink seaperch (*Zalembius rosaceus*) tended to avoid the beam. However, many species that typically associate with natural rocky outcrops, such as bocaccio (*S. paucispinis*), cowcod (*S. levis*), copper (*S. caurinus*), greenblotched (*S. rosenblatti*), pinkrose (*S. simulator*) and vermilion (*S. miniatus*) rockfishes, were found most often where the beam was exposed. In particular, a group of species (e.g., bocaccio, cowcod, blue (*Sebastes mystinus*), and vermilion rockfishes) called here the "sheltering habitat" guild, lived primarily where the beam was exposed and formed a crevice. This work demonstrates that the presence of sheltering sites is important in determining the species composition of man-made reefs and, likely, natural reefs. This research also indicates that adding structures that form sheltering sites in and around decommissioned platforms will likely lead to higher densities of many species typical of hard and complex structure.

Manuscript submitted 6 October 2004 to the Scientific Editor.

Manuscript approved for publication 14 December 2005 by the Scientific Editor.

Fish. Bull. 104:542–549 (2006).

Understanding the habitat preferences of deeper-water (below scuba depth) fishes has proven to be elusive. Off the Pacific Coast, several studies (Stein et al., 1992; Yoklavich et al., 2000; Nasby-Lucas et al., 2002) have demonstrated that habitat characteristics play a major role in shaping deeper-water fish assemblages. In those studies it was apparent that, although individuals of many species may be found in a number of habitats, most species showed distinct preferences. These studies clearly showed the role that hard structure plays for many species. How more subtle habitat characteristics, such as the presence of sheltering sites, may influence species composition was still unclear.

Between 1995 and 2002 we surveyed fish assemblages associated with southern California oil and gas platforms. Platforms may serve at least two functions for these fishes. First, the water column around many platforms serves as a nursery ground for a suite of rockfishes (*Sebastes* spp.) and other fish species, often harboring higher densities of these species than do nearby natural outcrops (Love et al., 2003). Second, platform bottoms, where the platform jacket and well pipes meet the sea floor, may harbor high densities of subadult and adult fishes. Most of these fishes are rockfishes, but lingcod (*Ophiodon elongatus*), painted greenling (*Oxylebius pictus*), and various members of the surfperch family (Embiotocidae) may also be abundant (Love et al., 1999; Love et al., 2003).

The platforms we surveyed were designed to have large, circular (1 m in diameter) horizontal beams that connect vertical and diagonal jacket elements at or near the sea floor. In some instances, these beams were buried, either by shells that had fallen from shallow parts of the jacket or by a combination of shells and fine sediment. In other instances, beams were partially exposed (full width of beam or partial width of beam was resting on the sea floor) or completely exposed (thus leaving a gap between the beam and sea floor). During our fish surveys, we noted that fishes appeared to be patchily distributed along the platform bottom and that some species seemed to be responding to the presence or absence of the beam and to the amount of space under the beam. Because the beams are all composed of similarly shaped steel and differ only in the amount of surface exposed, we hypothesized that patterns of fish associations with this structure would present insights into the role that sheltering spaces play in determining species assemblages in both natural and man-made habitats.

Materials and methods

Field sampling

Between 1996 and 2002, we surveyed fish assemblages around seven oil and gas platforms in southern and central California (Table 1, Fig. 1) using the *Delta* research submersible, a 4.6-meter, 2-person vessel, operated by Delta Oceanographics of Oxnard, California. Aboard the *Delta,* we conducted belt transects about two meters from the platform while the submersible maintained a speed of about 0.5 knots. Surveys were conducted in fall, in order to optimize good weather and water clarity.

Submersible surveys were conducted during daylight hours between one hour after sunrise and two hours before sunset. During each transect, a researcher made observations from a viewing port on the starboard side of the submersible. An externally mounted hi-8 mm video camera with lights filmed the same viewing field as seen by the observer. The researcher identified, counted, and estimated the lengths of all fishes and verbally recorded those data on the video. All fishes in a volume two meters from sea floor upwards and two meters from the submersible outwards were counted. Fish lengths were estimated by using a pair of parallel lasers mounted on either side of the external video camera. The projected reference points were 20 centimeters apart and were visible to both the observer and the video camera.

We defined the amount of beam exposure on a scale of 0–4: 0=the beam was completely covered by shells and soft sediment and it was not visible; 1=only the top of the beam (usually encrusted with invertebrates) was visible; 2=the beam was partially exposed (top and sides)—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; and 4=the beam was completely exposed and formed an open crevice more than 0.5 m high (Fig. 2). For each fish we recorded the size of the gap with which the fish associated.

An environmental monitoring system aboard the submersible continuously recorded date, time, depth, and altitude above the sea floor of the vessel. These environmental data were overlaid on the original videotape upon completion of each survey. Transect videos were reviewed aboard the research vessel or in the laboratory and observations transcribed into a database.

Statistical analysis

We were interested in broad patterns of species' distribution among small-scale habitats. Because rare species may prefer some (nonmeasured) extreme habitat and thus potentially would have skewed a general picture, we did not use those species where fewer than 40 fish were seen or those that were not seen on at least five dives. This left us with 27 species (of the original

Table 1

Platforms, bottom depths, crossbeam exposure parameters, and numbers of fishes surveyed in this study. Beam exposure scale: 0=beam was completely covered and not visible; 1=only the top of the beam was visible; 2=the beam was partially exposed—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; 4=the beam was completely exposed and formed an open crevice more than 0.5 m high.

Platform	Years	Depth (meters)	Amount of platform covered (0) or exposed (1–4) (length in meters, percent of total in parentheses)					Total amount of beam (covered and exposed, in meters)	Mean gap size (and standard deviation)	Number of fishes
			0	1	2	3	4			
Irene	1996–2001	73	422 (33.9)	142.2(11.4)	449.9(36.2)	229.5(18.5)	0	1243.6	1.4(0.8)	10,591
Hidalgo	1996–2001	130	146.9(9.3)	458.9(29.2)	478.1(30.2)	499.8(31.6)	0	1583.8	1.8(0.9)	11,509
Harvest	1996–2000	205	934.8(73.9)	172.9(13.7)	80.8(6.4)	76.9(6.1)	0	1265.5	0.5(0.4)	775
Hermosa	1996–2000	183	235.5(18.4)	721.3(56.4)	299(23.4)	24.2(1.9)	0	1279.9	1.1(0.6)	7195
Holly	1996–1999, 2001	64	744.4(71.0)	82.2(7.8)	82.8(7.9)	126.6(12.1)	12.7(1.2)	1048.7	0.7(0.6)	4196
Grace	1996, 1997, 1999–2002	96	512.2(32.4)	17.7(1.1)	81.3(5.1)	484.5(30.6)	486.9(30.8)	1583.1	2.3(1.3)	16,688
Gail	1996, 1997, 1999–2002	224	68.8(3.8)	4.8(0.3)	774.4(43.0)	951.4(52.9)	0	1799.5	2.5(1.1)	2045
Total			3064.5	1600.1	2246.9	2393.0	499.5	9804.1		52,999

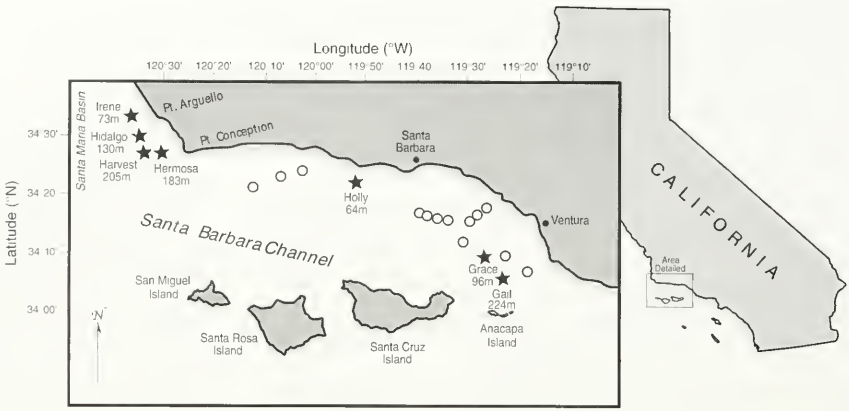

Figure 1

Location of platforms in the Santa Barbara Channel and Santa Maria Basin. Platforms discussed in this paper are shown as black stars and their bottom depths are indicated. The open circles indicate other platforms.

65) and 50,048 fish of the original 52,999 observations, or 95.1% of fish observed on all dives. In our analyses, we separated bocaccio (*Sebastes paucispinis*) and lingcod into two categories, YOY and older fishes, based on length-at-age and length-at-first-maturity data (Miller and Geibel, 1973; Cass et al., 1990; Love et al., 2002).

We used chi-square goodness-of-fit tests to determine which species tended to avoid or favor certain beam habitats. Species tend to be associated with particular depth ranges, platforms are placed at fixed depths, and some species may or may not have ever been observed on some platforms. Thus, the proportion of a particular beam habitat available to a given species was determined as the proportion of that habitat occurring only on those platforms where the species was observed. We hypothesized that if a particular species does not favor or avoids certain habitats, the expected number of those fish seen in particular habitats would be proportional to the amount of available habitat. In equation form: Let $u_{j,j}$ be the proportion of gap j (j=0, 1, 2, 3, or 4) available to species i (i=1, 2..., 27) and T_i be the total number individuals of species i observed. Then, the expected number of fish i at gap j, $E_{j,i} = u_{j,i} \times T_i$. Under the null hypothesis for species i,

$$X_i^2 = \sum_{j=0}^{4} \frac{(O_{j,i} - E_{j,i})^2}{E_{j,i}}$$

is distributed as a chi-square random variable with n_i–1 degrees of freedom, where n_i is the number of u_{ij}>0. The asymptotic assumptions for the chi-square test are not valid if the expected value of many cells is small. Cochran (1954) developed a conservative rule of thumb that the test not be used if more than 20% of the expected cell frequencies are less than five. Koehler and Larntz (1980) suggested that the chi-square test is reasonable if the total number of observations is greater than 10, the number of categories is at least 3, and the square of the number of observations is greater than 10 times the number of categories.

If the goodness-of-fit hypothesis was rejected, we examined the individual deviations, $X_{ji} = (O_{ji} - E_{ji})/(E_{ji})^{.5}$, which are approximately distributed as normal (0,1) random variables under the null hypothesis. Small values of X_{ji} indicate that the species is found less often than predicted, whereas large values indicate it is found more often.

Results

All species satisfied both the Cochran (1954) and Koehler and Larntz (1980) criteria for the validity of the chi-square test (Table 2). The null hypothesis that species are randomly distributed among the crevice habitats was rejected (P<0.0001) for all but one species, kelp greenling (*Hexagrammos decagrammus*) (Table 2).

We surveyed a total of 9804.1 m^2 of sea floor. Platforms varied both in the amount of horizontal beam exposed and, when exposed, the degree of gap between beam and sea floor. At each platform, there was relatively little annual variability in the amount of beam exposed or the size and type of gap (Fig. 3). Mean size of gap per platform over the entire study ranged from 2.5 (SD=1.1) to 0.5 m (SD=0.4). (Fig. 3, Table 1). Platforms Gail and Grace, in the east Santa Barbara Channel, had the greatest amount of gap. In particular, almost none of the bottommost beam at Gail was completely buried and most of it was at least partially exposed. At the

Figure 2

Examples of four types of bottom beam structure: (**A**) at least some of the beam was visible, but the full width of the beam rested on the sea floor (greenspotted rockfish, *Sebastes chlorostictus*); (**B**) the beam was partially exposed, remaining in contact with the sea floor at its bottom, not its sides (flag rockfish, *S. rubrivinctus*); (**C**) the beam was completely exposed and formed an open crevice less than 0.5 m high (cowcod, *S. levis*); (**D**) the beam was completely exposed and formed an open crevice more than 0.5 m high (vermilion rockfish, *S. miniatus*).

other extreme, most of the bottom beam at both Platforms Holly in the central Santa Barbara Channel and Harvest, off Point Conception, was completely buried. We saw little relationship between geographic location (or platform depth) and mean gap size. For instance, Platforms Hidalgo and Harvest are located within 4.6 km of each other, yet have very different beam exposures, as do Platforms Holly and Irene that are sited at almost the same depth. A lack of relationship probably reflects differences in oceanographic conditions, because some of these structures are found in areas where strong currents scour the bottom, whereas others are found in areas where sediments have not been disturbed.

Except for kelp greenling, all species exhibited some beam habitat preference (Table 2). Species found more often where the beam was completely buried (gap 0) included greenstriped (*S. elongatus*), non-YOY lingcod, rosy (*S. rosaceus*), sharpchin (*S. zacentrus*), and stripetail (*S. saxicola*) rockfishes, painted greenling, pink seaperch (*Zalembius rosaceus*), and sanddabs (*Citharichthys* spp.). Those that favored the presence of the beam or some amount of exposure (exposures 1 and 2) included calico (*S. dallii*), copper (*S. caurinus*), flag (*S. rubrivinctus*), and pinkrose (*S. simulator*) rockfishes, pile perch (*Rhacochilus vacca*), and sharpnose seaperch (*Phanerodon atripes*). Species that tended to inhabit areas where there was a gap between beam and sea floor (exposures 3 and 4) were blue (*S. mystinus*), brown (*S. auriculatus*), canary (*S. pinniger*), greenblotched (*S. rosenblatti*), halfbanded (*S. semicinctus*), squarespot (*S. hopkinsi*) and vermilion (*S. miniatus*) rockfishes, and both size classes of bocaccio (*S. paucispinis*). The vast majority of cowcod (*S. levis*) were found at beams that were scored as exposures 2 and 3. Both greenspotted rockfish (*S. chlorosticus*) and YOY lingcod appeared to prefer either soft bottom without beam exposure or beam exposure without a deep gap (exposures 1 and 2).

Table 2

The observed number of fish at each exposure value, the expected number under the null hypothesis, and the chi-square statistics of goodness of fit. Observed values are coded in the following manner: 1) "– –" if X_{ij} <–4; indicating that the observed value is much smaller than predicted (P=0.0001), 2) "–" if –2 <X_{ij} <–4; indicating that the observed value is smaller than predicted, (P=0.05), 3) "+" if 4 <X_{ij} <2; indicating that the observed value is larger than predicted, (P=0.05), 4) "+ +" if X_{ij} >4; indicating that the observed value is much larger than predicted, P = 0.0001. Beam exposure scale: 0=beam was completely covered and not visible; 1=only the top of the beam was visible; 2=the beam was partially exposed—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; 4=the beam was completely exposed and formed an open crevice more than 0.5 m high.

	Observed number of fish at each exposure scale value						Expected number of fish at each exposure scale level					χ^2 test of null hypothesis		
Species	0	1	2	3	4	Total	0	1	2	3	4	df	χ^2	P
Blackeye goby	64 +	1	0 –	2 –	0	67	47.6	5.2	5.3	8.1	0.8	4	19.81	<0.001
Blue rockfish	13 – –	0 – –	8 –	29	55 + +	105	45.5	6.6	16.6	22.8	13.5	4	162.99	<0.001
Bocaccio (>20 cm)	16 – –	2 – –	210 – –	458 + +	138 + +	824	229.8	87.8	205.6	247.2	53.7	4	595.27	<0.001
Bocaccio (yoy)	11 – –	5 – –	8 – –	205 + +	0	229	57.1	38.3	58.1	62.1	13.4	4	451.43	<0.001
Brown rockfish	23	6	30	57 + +	0	116	59.0	11.4	27.0	18.0	0.6	4	109.81	<0.001
Calico rockfish	444 – –	168 + +	379 + +	112 – –	4	1107	563.3	108.4	257.2	172.0	6.1	4	137.34	<0.001
Canary rockfish	9 –	15	24	42 + +	4	94	28.7	19.8	19.4	19.0	7.0	4	44.80	<0.001
Copper rockfish	460 – –	192 + +	530 + +	296	3 – –	1481	641.5	92.5	234.8	321.3	190.9	4	716.18	<0.001
Cowcod	9 –	0 –	26 +	31 +	0	66	20.2	13.6	16.2	15.9	0.0	4	40.2	<0.001
Flag rockfish	88 – –	42 –	195 + +	134	12	471	147.2	76.9	107.9	115.0	24.0	4	119.00	<0.001
Greenblotched rockfish	49 – –	23 – –	304 + +	181 +	0	557	140.7	102.0	127.1	151.0	36.1	4	409.20	<0.001
Greenspotted rockfish	120 + +	329 + +	656 + +	243 – –	13 – –	1361	425.4	222.1	311.9	332.2	69.3	4	719.98	<0.001
Greenstriped rockfish	130 + +	67	84	54 –	0	335	78.3	76.7	92.2	87.7	0.0	3	49.04	<0.001
Halfbanded rockfish	4457 – –	7338	3142 – –	15,838 + +	5593 + +	36,368	13,610.8	7247.9	6690.1	6549.6	2269.6	4	26,078.39	<0.001
Kelp greenling	14	8	8	8	4	42	14.0	5.4	8.4	10.3	3.8	4	1.80	0.772
Lingcod (>20 cm)	128 +	26 –	91	88	8	341	106.6	55.7	78.2	83.2	17.4	4	27.54	<0.001
Lingcod (yoy)	201 + +	54	111 + +	16 – –	2 – –	384	143.7	76.5	70.6	69.2	24.0	4	113.52	<0.001
Painted greenling	104 + +	38 +	50	37 – –	5 –	234	61.1	22.8	60.2	73.9	16.1	4	68.19	<0.001
Pile perch	29 – –	45 + +	41	37 +	0	152	77.3	14.9	35.3	23.6	0.8	3	100.52	<0.001
Pinkrose rockfish	5 – –	11 – –	182 + +	47	0	245	69.9	50.7	65.1	59.3	0.0	3	303.86	<0.001
Pink seaperch	60 + +	1 –	6	4 –	3 –	74	28.2	15.5	8.8	12.0	9.4	4	59.99	<0.001
Rosy rockfish	61 +	12	19	29	3 –	124	41.5	15.9	24.8	30.4	11.3	4	17.74	<0.001
Sharpchin rockfish	42 + +	14	5 –	0 –	0	61	14.3	14.0	16.8	16.0	0.0	3	78.22	<0.001
Sharpnose seaperch	7 – –	205 + +	168 + +	31 – –	0	411	209.1	40.2	95.5	63.8	2.3	4	944.19	<0.001
Squarespot rockfish	186	4 – –	54 – –	237 + +	21 –	502	167.9	64.5	100.5	123.3	45.9	4	198.65	<0.001
Stripetail rockfish	197 + +	37 –	65 + +	152	0	451	111.6	61.8	129.4	148.3	0.0	3	107.37	<0.001
Unidentified sanddab	76 + +	0 –	0 –	2 – –	2 –	80	26.4	4.5	15.0	20.2	13.8	4	138.96	<0.001
Vermilion rockfish	230 – –	162 – –	525 + +	582 + +	437 + +	1936	647.4	248.6	387.5	475.4	177.2	4	753.15	<0.001
Widow rockfish	1295	53 – –	68 – –	466 –	87 –	1969	491.1	329.1	499.5	534.1	115.2	4	1935.80	<0.001

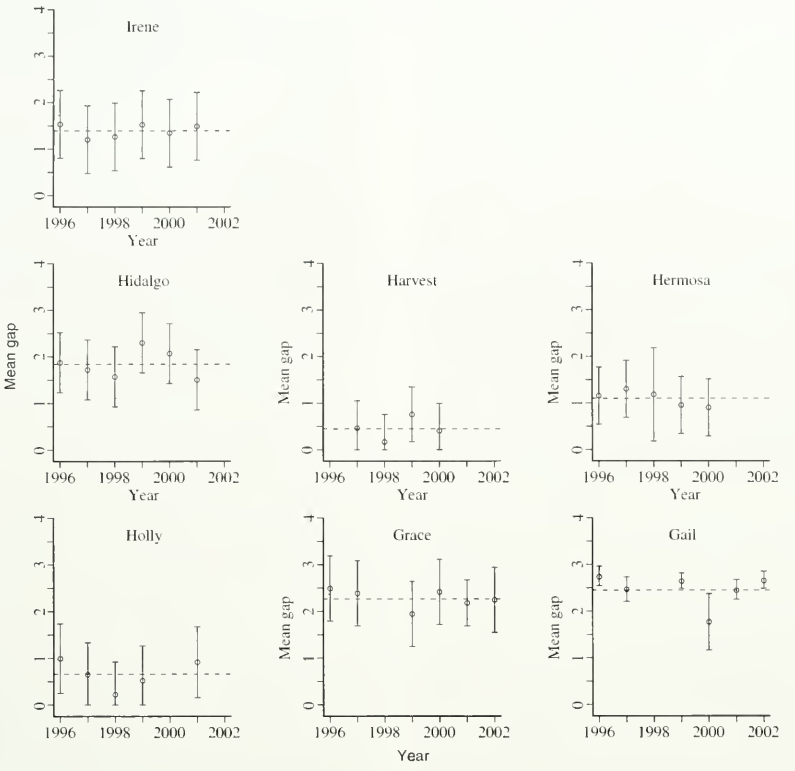

Figure 3

Mean size of gap between beam and sea floor on a scale of 0–4 at each platform, by year. Platforms are ordered from northernmost to southernmost. 0=beam was completely covered and not visible; 1=only the top of the beam was visible; 2=the beam was partially exposed—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; 4=the beam was completely exposed and formed an open crevice more than 0.5 m high.

Many species appeared to avoid certain beam configurations; that is, they were found in numbers far less than expected by chance. For instance, blue, flag, greenblotched, halfbanded, pinkrose, squarespot, and vermilion rockfishes, and bocaccio were all significantly less abundant in areas with either no horizontal beam or where that structure was not well exposed (exposures 0 and 1). On the other hand, a variety of taxa, such as greenspotted rockfish, YOY lingcod, painted greenling, and sanddabs were relatively uncommon where there was a large gap between the bottom of the beam and the sea floor (exposure 4). Widow rockfish (*S. entomelas*), in our study comprising almost entirely YOY individuals, tended to avoid areas where the beam was exposed. Calico and copper rockfish, along with sharpnose seaperch, tended to avoid both sea floors with no beam present and sea floors where the beam structure was completely exposed (and the gap was significant).

Discussion

Species generally occupied those parts of the beams that appear to be most similar to their natural habitats (Feder et al., 1974; Yoklavich et al., 2000, 2002; Love et al., 2002). In our system, there was a suite of species that were less abundant or nearly absent when the beam was exposed. These species included blackeye goby

(*Rhinogobiops nicholsii*), greenstriped, sharpchin, and stripetail rockfishes, painted greenling, pink seaperch, and sanddabs. These species are usually referred to as "soft substrata" or "mixed substrata" fishes. Other taxa were associated more often or almost exclusively with the exposed beam and these are species often categorized in the literature as "reef" species. These included blue, brown, calico, canary, copper, flag, greenblotched, halfbanded, pinkrose, squarespot, and vermilion rockfishes, cowcod, bocaccio, pile perch, and sharpnose seaperch. As in natural systems, to a great extent greenspotted rockfishes and non-YOY lingcod inhabited several different habitats.

There is evidence that the crevices, cracks, and caves on both natural and human-made structures, may influence fish species assemblages because they form shelters for fishes (Luckhurst and Luckhurst, 1978; Kellison and Sedberry, 1998; Rilov and Benayahu, 1998). In many instances, overall fish abundances are positively correlated with these openings that enhance habitat complexity. On the Pacific Coast, there are only a few observations specifically addressing shelter sites and deeper-water fishes. Caselle et al. (2002), surveying oilfield debris off southern California, examined the influence that structural complexity may exert on fish assemblages. They found that the presence of shelter was one of the most important determinants for high densities of both copper and vermilion rockfishes and played some role in the abundance of a number of other species. Yoklavich et al. (2000) noted that the "rock habitat guild," composed of such species as cowcod, pygmy (*S. wilsoni*), and yelloweye rockfishes, were "closely associated with ledges, caves, crevices, and overhangs." Discussing yelloweye rockfish habitat off southeastern Alaska, O'Connell and Carlile (1993) stated that the "occurrence of refuge spaces may be one key to the presence of yelloweye rockfish, which were normally found in areas where refuge spaces were available, even if the surrounding habitat was not their preferred habitat of boulder or broken rock."

From our research, it was apparent that, among the reef species, there is a "sheltering" guild. These are species (i.e., blue, canary, flag, greenblotched, halfbanded, pinkrose, and vermilion rockfishes, cowcod, and bocaccio) for which an exposed beam alone is not sufficient. These taxa tend to be associated with the spaces that provide shelter under that structure. Blue, brown, canary, halfbanded, and vermillion rockfishes and bocaccio were found in particularly large numbers where the gap between beam and sea floor was largest (exposures 3 and 4). A few species, such as calico, copper, greenspotted, and pinkrose rockfishes, YOY lingcod, and sharpnose seaperch, although often found along the beams, seemed to avoid the most exposed sections.

Fishes that either avoided the beam, or at least that part that formed a gap between the beam and the sea floor, tended to be small in size and to fall into several categories. One group, the sanddabs, is adapted to living on soft substrata. Other species, including blackeye goby, greenstriped, rosy, and sharpchin rockfishes, painted greenling, and pink seaperch, are diminutive and solitary. Although pink seaperch are found in schools over natural outcrops, we did not see them schooling around platforms. All of these diminutive forms will live in high relief, complex substrata when larger predators have been removed from the system, as occurs on most of the rocky outcrops off southern and central California (M. Love, unpubl. data). However, it is likely they avoid exposed beams because of the presence in the area of high densities of large fishes.

Variability in habitat complexity, caused by variation in the amount of beam exposure and the size of gap between beam and sea floor, may explain at least one of the between-platform differences we have observed in fish assemblages. In general, platforms occupying similar depths harbor similar fish assemblages (Love et al., 2003). However, an exception was found when comparing fish species at Platform Gail (224 m) and at Platform Harvest (205 m) (Love et al., 2003). In order of density, greenblotched rockfish, bocaccio, greenspotted, stripetail, and pinkrose rockfishes dominated the bottom fish assemblage at Platform Gail. Cowcod, although not among the top five most abundant fish, were found at higher densities at this platform than at any natural outcrops or other platform that we surveyed in southern California. By contrast, at Platform Harvest, stripetail, greenstriped, greenspotted, greenblotched, and sharpchin rockfishes were most commonly seen. Cowcod were considerably less abundant at this platform and we observed almost no bocaccio. Platform Gail contains, on average, the highest mean exposure value (about 2.5 m) and Harvest the lowest (slightly more than 1.0 m). Most of the common fishes at Gail are representative of complex habitat, those at Harvest of lower relief and softer substrata.

This research may have a bearing on the ultimate disposition of California platforms. The possibility of enhancing fish habitats and fish populations at platforms is an important issue in the decommissioning process. In particular, the California Department of Fish and Game has suggested increasing habitat complexity around the bottom of platform jackets by placing quarry rock or other materials around the jacket (Schroeder and Love, 2004). However, to date, augmentation has not been attempted. With the results from our study, we predict that increasing the habitat complexity at platforms will, in some instances, increase the densities of a number of rock or boulder-oriented species, those species that are preferentially found where there is a gap below the bottom beam.

In addition, the results of this research may also be applied to natural reef studies, particularly those involving marine protected areas (MPAs). This research clearly demonstrates that, in terms of habitat preferences of many fish species, not all hard habitat is the same. In fact, this research indicates that it may be possible to predict which species are found around different types of hard structure by the presence

of different types of shelters at the hard structure. This would be particularly important when deciding on what habitats to set aside for MPAs designed to protect and enhance the populations of specific fish species.

Acknowledgments

We thank Ann Bull, Lyman Thorsteinson, and George Steinbach for their support of this research. This research was funded by the Biological Resources Division, U.S. Geological Survey (National Offshore Environmental Studies Program 1445-CA-0995-0386), Minerals Management Service, and the California Artificial Reef Enhancement Program. Robert Lea, Mary Nishimoto, Linda Snook, Rick Starr, and Mary Yoklavich conducted some of the surveys and Linda Snook managed the survey data.

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A Bayesian method for identification of stock mixtures from molecular marker data

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Abstract—Molecular markers have been demonstrated to be useful for the estimation of stock mixture proportions where the origin of individuals is determined from baseline samples. Bayesian statistical methods are widely recognized as providing a preferable strategy for such analyses. In general, Bayesian estimation is based on standard latent class models using data augmentation through Markov chain Monte Carlo techniques. In this study, we introduce a novel approach based on recent developments in the estimation of genetic population structure. Our strategy combines analytical integration with stochastic optimization to identify stock mixtures. An important enhancement over previous methods is the possibility of appropriately handling data where only partial baseline sample information is available. We address the potential use of nonmolecular, auxiliary biological information in our Bayesian model.

Manuscript submitted 13 February 2005 to the Scientific Editor's Office.
Manuscript approved for publication 14 December 2005 by the Scientific Editor.
Fish. Bull. 104:550–558 (2006).

Stock mixture analysis using multilocus genotypes of fish is recognized as a versatile tool in fisheries management. The efficiency of combining polymorphic molecular markers, such as microsatellites, with a model-based approach to estimate stock mixtures, has been clearly demonstrated in the literature (Kalinowski, 2004; Reynolds and Templin, 2004). Since the beginning of the 21st century, Bayesian methods have largely replaced the earlier applied maximum likelihood approach based on latent class mixture models (Pella and Masuda, 2001). A similar trend has been true for the estimation of genetic population structure in general (e.g., Pritchard et al., 2000; Corander et al., 2003, 2004; Beaumont and Rannala, 2004). For an earlier approach to mixture analysis with incomplete information about source populations, see Smouse et al. (1990).

Bayesian methods for estimation of stock mixtures has generally been based on exploitation of data augmentation through Markov chain Monte Carlo (MCMC), where latent origins of caught individuals and values of the other model parameters are successively simulated from the corresponding posterior distributions. Such an approach is capable of avoiding certain estimation problems caused by missing data and rare alleles, which severely affect the maximum likelihood method. However, because of numerical deficiencies, there are situations where the MCMC based method for the latent class mixture model may easily fail to provide appropriate estimates. First, in the presence of very small groups of individuals representing some stock sources, the posterior distribution of the origins for these particular individuals and the corresponding posteriors of the source allele frequencies will typically comprise a high level of uncertainty. Consequently, the resulting MCMC simulation error in the estimates may be considerable. Second, when there are baseline samples available only for a subset of potential stock sources, estimation of origins is not feasible (Pella and Masuda, 2001). Use of the standard approach with a fixed number of sources, based on the available baseline samples, may easily lead to spurious estimates when there are individuals representing several additional sources in the data. Similarly, it is difficult to detect outlier individuals with the latent class approach with a fixed number of sources (Pritchard et al., 2000) because they are unlikely to be identified in the MCMC simulation for data sets of moderate to large size. Third, under partial baseline information, it is difficult to appropriately infer a suitable number of stock sources to represent a particular data set.

Partition-based Bayesian alternatives to latent class models for identification of genetic mixtures without baseline samples have recently been introduced (Dawson and Belkhir 2001; Corander et al., 2003, 2004). Corander et al. (2003, 2004) used an analytical integration strategy combined with stochastic search methods to make Bayesian estimation

more feasible when the number of genetically diverged sources contributing to the observed data is unknown. A wide variety of applications of this approach can be found in the literature (e.g., Heuertz et al., 2004, Seppä et al., 2004, Mäki-Petäys et al., 2005). The approach by Dawson and Belkhir (2001) is similar to that of Corander et al. (2004) in spirit; however, it is subject to two important limitations that prevent an efficient use of this approach in the current context. First, there are no readily available informative forms of the family of prior distributions used by Dawson and Belkhir (2001), which would be necessary for representing the baseline information. Second, their model formulation does not allow for missing alleles in the molecular marker data, which are present in most real data sets.

In our study, we extend the partition-based approach to incorporate *a priori* baseline information, making it suitable for identification of stock mixtures, either under complete or partial baseline sample information. Our focus is on the identification of the putative genetic mixture in the catch sample data, provided by the maximum *a posteriori* estimate of the assignment of the individuals into an unknown number of sources. Given the estimate, the proportions of the stocks in the population can be readily inferred by using the standard multinomial-Dirichlet model (e.g., Pella and Masuda, 2001) and generic Bayesian software, such as BUGS (Spiegelhalter et al., 2003), which has been widely used for fish population modeling (e.g., Meyer and Millar, 1999; Mäntyniemi and Romakkaniemi, 2002; Mäntyniemi et al., 2005).

Another novelty in our method is the possibility of using available biologically relevant information to pre-assign catch data into groups that can be considered as sampling units in the model. For instance, when the behavior of the investigated species is such that individuals obtained simultaneously at a single catch location are known to represent the same (yet unknown) stock, they can be allocated as a single unit to an origin. Such use of auxiliary information enhances the statistical power to detect the correct origin when the number of molecular marker loci available is limited. To illustrate our modeling approach, and to investigate its performance under various biological settings, we present results from several simulation experiments based partly on real molecular data for the Baltic Sea stock mixture of Atlantic salmon (*Salmo salar*).

Methods

Bayesian stock mixture model

In stock mixture estimation, there are typically available in samples two types of individuals, which are genotyped. One type consists of individuals with known origin (baseline data), and the other type represents a catch sample, which may have been pooled from several sources. Let m be the number of potential stocks, such that for each stock $i = 1,..., m$, there are n_i baseline individuals available. Furthermore, there may be an additional number of potential stocks contributing to the catch population; however, these are not represented by any baseline samples. We let K ($m \leq K$) denote the total number of potential stocks, which can have contributed to a catch sample of n individuals, whose origins are unknown. Notice that K is typically determined from the relevant biological information about the species under consideration. The target for our estimation is to infer the number of stocks, say k, having actually contributed to the catch sample, from the multilocus genotypes of both the baseline and catch individuals.

Under the assumption that the genetic information consists of N_L molecular marker loci, where at each locus $j = 1,..., N_L$, there are $N_{A(j)}$ different alleles distinguished among all baseline and catch samples. Pella and Masuda (2001) introduced a rather complicated empirical Bayes procedure to determine the prior distribution for the allele frequencies in the potential stocks through the observed genotypes of the baseline individuals (all stocks were assumed to be represented by baseline samples). Here we consider a simpler approach, by suitably modifying the standard Dirichlet prior used in Corander et al. (2003, 2004). We assume that the allele frequencies between marker loci are conditionally independent given the stock origins and consider the potential stocks to be in Hardy-Weinberg equilibrium (HWE).

Let p_{ijl} be the unknown frequency (or probability) of allele l in the stock i at locus j, given that k ($k \leq K$) stocks are considered. Further, for each locus $j = 1,..., N_L$, let α_{ijl} be a hyperparameter for a Dirichlet prior distribution of the allele frequencies of stock i ($i = 1,..., k; l = 1,..., N_{A(j)}$). Given the baseline information, we may partially update our beliefs about the allele frequencies using the posterior distribution derived from an initially vague reference prior. For each of the m stocks, where baseline samples are available, we set $\alpha_{ijl} = n_{ijl} + 1/N_{A(j)}$, where n_{ijl} is the observed number of copies of allele l at locus j among individuals in the baseline sample of size n_i. This hyperparameter updating procedure is standard in Bayesian analysis with the multinomial-Dirichlet model (Gelman et al., 2004). Correspondingly, for the other potential stocks, not represented by any baseline information, the count n_{ijl} is zero, and the hyperparameter is determined as $\alpha_{ijl} = 1/N_{A(j)}$.

A putative assignment of the catch data to the potential stocks is represented in our study by a partition-valued parameter $S = (s_1,..., s_k)$, which allocates the n individuals into k non-empty clusters. A cluster is labeled as either the corresponding baseline sample or, alternatively, as a group of unknown geographical origin. The prior distribution of the allocation parameter $P(S)$ is defined according to

$$P(S = (s_1,...,s_k)) = \begin{cases} c, \text{ if } k \leq K \\ 0, \text{ otherwise} \end{cases}, \quad (1)$$

which corresponds to a uniform distribution over the possible allocations of the catch individuals under the

restriction $k \leq K$. This particular prior specification allows a convenient estimation algorithm to be constructed for identifying those allocations associated with high posterior probabilities, given the molecular marker data. Also, our prior is considerably more informative from the biological perspective than the uniform prior with $K = n$ used in Corander et al. (2004) because it assigns a zero probability to most allocations that are very unrealistic for a moderate or large sample size n.

The posterior probability of an allocation S over the class of all putative candidates is defined as

$$p(S \mid data) = p(data \mid S)P(S) / \sum_{S \in \Im} p(data \mid S)P(S), \quad (2)$$

where $p(data \mid S)$ is the marginal likelihood of having the allele frequency parameters of each class s_i in S integrated out analytically (formula A1 in Corander et al., 2003) according to

$$p(data \mid S) = \prod_{i=1}^{k} \prod_{j=1}^{N_i} \left[\frac{\Gamma(\sum_l \alpha_{ijl})}{\Gamma(\sum_l \alpha_{ijl} + n_{ijl})} \prod_{l=1}^{N_{ij}} \frac{\Gamma(\alpha_{ijl} + n_{ijl})}{\Gamma(\alpha_{ijl})} \right], \quad (3)$$

where n_{ijl} is now the observed number of copies of allele l at locus j among catch individuals allocated to cluster i. The analytical integration approach was used earlier in a related genetic context by Balding and Nichols (1997), Rannala and Hartigan (1996), Rannala and Mountain (1997).

As can be seen from the above expression, the parameter that needs to be estimated in our stock mixture model is the allocation partition S. In situations where auxiliary biological information provides a pre-assignment of some catch individuals into *a priori* sampling units, each known to represent a single unknown origin, the above formula still applies. However, the prior distribution of the allocation parameter needs to be modified accordingly, to exclude the values of S that assign individuals in the same sampling unit to distinct origins.

Algorithm for allocation estimation

In the sequel, we consider the general situation where the catch data are represented by a number of *a priori* sampling units, each containing potentially more than a single individual (see the previous section). When no auxiliary information for pre-assignment to sampling units is available, each sampling unit will correspond to a single individual in the catch data.

The two main aspects of our stock mixture model that need to be estimated from marker data are the number of clusters (k) suitable for a particular data set, and the allocation of sampling units to the clusters. Corander et al. (2003, 2004) used various stochastic search strategies for estimation of a comparable model without prior baseline samples. In our study, we develop an alternative method to enable analyses of data sets ranging from moderate to challenging because the MCMC algorithms introduced by Corander et al. (2003, 2004) are computationally time and memory intensive. The central idea is to use a "greedy" stochastic search algorithm (Fletcher, 1987) to find a partition S with the highest posterior probability (Eq. 2). Repeated runs of the algorithm enable investigation of the stability of the estimation procedure, in a way that is similar to the parallel MCMC approach of Corander et al. (2004).

An initial partition for the algorithm is determined by assigning sampling units one by one to such a cluster, so that the resulting partition has the highest possible posterior probability. After specifying the initial partition, the greedy algorithm proceeds by performing the following operations repeatedly on the current partition:

1 The algorithm moves sampling units from one cluster to another. In a stochastic order, for each sampling unit, it calculates the change imposed to the posterior probability $P(S \mid data)$ by moving the particular sampling unit to any of the other clusters, including even an empty cluster, unless that would lead to $k > K$. It moves the sampling unit to the cluster that increases the value of $P(S \mid data)$ most (if no increase is possible, the sampling unit is not moved).
2 It joins clusters. For each pair of clusters, the algorithm calculates the change to $P(S \mid data)$ imposed by joining them. It joins the two clusters that cause the maximal increase (if no increase is possible, no clusters are joined).
3 It splits clusters. Using the Kullback-Leibler divergence between sampling units (Corander et al., 2003), the algorithm splits each cluster into maximally 20 subclusters and calculates the change to $P(S \mid data)$ imposed by keeping one of the introduced subclusters as a separate new cluster, or by joining it to any of the previously existing clusters. It keeps the new configuration that improves the value of $P(S \mid data)$ most (if no improvement is possible the split is not made).
4 It splits clusters into exactly two maximally homogeneous subclusters with the Kullback-Leibler divergence, otherwise analogously as in step 3.
5 It re-allocates several sampling units from a cluster. In a stochastic order, for each cluster, the algorithm orders the sampling units of the cluster such that the first sampling unit is the one whose removal from the cluster would improve the marginal likelihood of the cluster most, and so on. A putative candidate for a new partition is formed by moving sampling units one by one to some other cluster, such that the $P(S \mid data)$ of the resulting partition is as high as possible (these moves are performed even if a single move results in a worse solution). If at some point the total change in $P(S \mid data)$ is positive, the putative candidate is accepted and operation 5 is completed. When the total change remains negative, even after re-allocation of all the sampling units in a single cluster, the putative candidate is rejected and another cluster is chosen as a target until all clusters have been considered.

The optimization operations are repeated in a varying order, until none of them improves the posterior probability $P(S|data)$ of the current partition. The allocation of sampling units to different clusters is based on the obtained partition, and the suitable number of clusters k is estimated from the partitions visited during the simulation.

Measurement of the strength of evidence for any particular value of the partition S, given the marker data, is an intricate process, in particular for large data sets from complex stock mixtures. Theoretically, the unknown largest posterior probability may be extremely small, even in situations where a particular model provides an adequate fit to the observations. An important factor explaining such a feature is the large number of possible allocations, which all have positive posterior probabilities by definition. This feature is of general concern in a Bayesian analysis that comprises vast model spaces, see, e.g., the discussion in Madigan and Raftery (1994). Because the actual estimated value of the posterior probability may be an intuitively misleading goodness-of-fit measure, we use an alternative strategy for characterization of the uncertainty in relation to the estimated allocation.

Bayes factors (e.g., Kass and Raftery, 1995) provide a computationally efficient approach to local assessment of the amount of the peak of the posterior distribution around an estimate of S. Let S^* denote an alternative allocation obtained from an estimate S by moving any particular sampling unit to another putative stock. The strength of evidence in favor of placing that sampling unit in the original stock against placement in the new stock is provided by the Bayes factor

$$B_{S,S^*} = \frac{p(data \mid S)P(S)}{p(data \mid S^*)P(S^*)}, \quad (4)$$

which measures how many times more plausible the allocation S is for the particular sampling unit. When the value of Equation 4 is small, say $B_{S,S^*} < 10$ (or $\log_e B_{S,S^*} < 2.3$, Kass and Raftery, 1995), the data do not strongly support a single origin for the particular sampling unit. Because calculation of these Bayes factors is computationally inexpensive, they can be easily provided for every possible sampling unit or stock combination.

In addition to Bayes factors, conditional posterior probabilities for the allocation of each individual over the range of different putative stocks identified through S can be used to characterize the uncertainties in the Bayesian estimate. The conditional posterior probability distribution is defined for each individual by

$$P(S_i \mid data) = \frac{p(data \mid S_i)P(S_i)}{\sum_{i=1}^{k} p(data \mid S_i)P(S_i)}, \quad (5)$$

where S_i denotes that the particular individual is allocated to the ith class of S (over the k possible alternatives). When only a single stock has a high conditional posterior probability, the allocation is made on a firm basis. However, when at least two sources are identified with reasonably high posterior probabilities, the genetic evidence is not conclusive enough for a classification of the particular individual to a single source. The advantage of the conditional posterior probabilities over Bayes factors in characterization of the classification uncertainty for each individual is that the former compares simultaneously all putative sources, whereas the latter provides only a pairwise judgement.

The correct number of clusters needed to describe the data can be estimated from the partitions that were visited during the simulation. During the simulation the algorithm stores the marginal likelihoods and the sizes of the 30 best visited partitions, and the posterior probabilities for the different numbers of clusters can then be estimated analogously to those estimated by Corander et al. (2004). Usually, if there is a lot of molecular data available (e.g., hundreds of loci have been observed) only a few of the best partitions have influence on the computed posterior probabilities because the relation of marginal likelihoods between different partitions can be up to ~exp(1000). If the data are sparse (e.g., only about 10–20 loci have been observed) and only partial baseline information is available, the uncertainty related to the correct number of clusters can be considerable because many partitions with differing sizes and approximately equal marginal likelihood may be found. In these cases, to obtain a more reliable estimate of the correct number of clusters, the algorithm should be run multiple times with different upper bounds (K) in order to facilitate the identification of those partitions that have real influence in the posterior probabilities. In our implementation of the estimation algorithm, we have included the possibility to automatically process information from multiple runs.

Empirical illustration of the partition-based approach

The Bayesian estimation algorithm described in the previous section is implemented in BAPS software.[1] The examples considered here are produced by BAPS analyses of data simulated by using the real data from Koljonen et al. (2002), who assessed allele frequencies for nine microsatellite markers in Atlantic salmon within the Baltic Sea region. We have experimented with several simulation configurations to investigate how our method would be expected to perform under a variety of biological conditions.

The five wild stocks of Atlantic salmon considered in Koljonen et al. (2002) correspond to five different rivers draining into the Baltic Sea: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The pairwise genetic distances (Nei's D_A, Nei et al., 1983) between these stocks underlying our simulations are

[1] BAPS software is freely available at URL http://www.rni.helsinki.fi/~jic/bapspage.html. Results presented here were calculated with version 3.1 (release date 5 March 2005).

given in Table 1 (reproduced from Koljonen et al., 2002). An estimate of total F_{ST} (Weir and Cockerham, 1984) equal to 0.07 was obtained in Koljonen et al. (2002) for these stocks on the basis of the nine microsatellite loci. The magnitude of the genetic differentiation in the underlying population is fairly small, and the pairwise distances vary considerably. Thus, we may conclude that these stocks represent a biologically challenging setting for inference about the genetic mixture in a population sample. Using the individual stock allele frequencies, we have simulated baseline individuals and catch samples under the assumptions of HWE and no linkage between the loci. A wide variety of configurations, with complete and partial baseline information and different sample sizes, were tested. In the analyses involving five underlying stocks, we used $K = 10$ as the prior upper bound, and the estimation algorithm was run 12 times for each replicate data set. For cases with only two underlying stocks, the upper bound was set as $K = 6$.

Results of our simulation experiments are summarized in Tables 2–8. As a summary, we highlight the following aspects. Uneven proportions of stock presence in the samples do not seem to affect the inference notably, even when the baseline information is only partial. The results in Table 3 are produced under a particularly challenging situation, where the baseline information comprises 40 individuals from a single stock only. The sample configuration then contains 40 individuals from this stock and 10 individuals from another, *a priori* unknown stock. The results show that our method performs surprisingly well in the identification of the outgroup, given that the genetic difference between the two underlying stocks is not negligible. However, as the results in Table 4 illustrate, the presence of putative stocks not represented by baseline information may also be masked by the baseline available for a genetically similar stock. Identification of putative stocks without using any baseline information may *de facto* be more successful under such circumstances (compare Tables 4a–4d). Therefore, we suggest that in practice both types of analyses are performed and the results compared, since this is computationally inexpensive with our method. Our results indicate that incomplete baseline information is expected to be most fruitful for the identification task when there are baseline samples available from the stocks that are genetically most similar. The baseline configurations in Table 4 can be

Table 1

Pairwise genetic distances (Nei's D_A, Nei et al., 1983) between different Atlantic salmon stocks within the Baltic Sea region (reproduced from Table 2 in Koljonen et al., 2002). Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.

Stocks	TornW	Simo	Ii	Oulu
Simo	0.129			
Ii	0.068	0.125		
Oulu	0.110	0.164	0.131	
Neva	0.261	0.285	0.284	0.261

Table 2

Allocation average percentages over 20 simulations, when 25 individuals from each stock were present in the sample data, and the number of baseline individuals available from each stock was (**A**) 30, (**B**) 15, and (**C**) 5. The column with the heading "Other" refers to additional stocks inferred by the method. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.

		Allocation					
Origin		TornW	Simo	Ii	Oulu	Neva	Other
A	TornW	0.80	0.01	0.15	0.03	0.00	0.00
	Simo	0.03	0.95	0.02	0.00	0.00	0.00
	Ii	0.11	0.02	0.84	0.03	0.00	0.00
	Oulu	0.03	0.01	0.01	0.95	0.00	0.00
	Neva	0.00	0.00	0.00	0.00	1.00	0.00
B	TornW	0.72	0.03	0.18	0.06	0.00	0.00
	Simo	0.02	0.94	0.02	0.02	0.00	0.00
	Ii	0.11	0.03	0.84	0.02	0.00	0.00
	Oulu	0.04	0.01	0.03	0.91	0.00	0.00
	Neva	0.00	0.00	0.00	0.00	0.99	0.00
C	TornW	0.59	0.06	0.23	0.09	0.01	0.02
	Simo	0.04	0.90	0.04	0.01	0.00	0.00
	Ii	0.20	0.06	0.70	0.03	0.00	0.01
	Oulu	0.03	0.01	0.05	0.91	0.00	0.00
	Neva	0.00	0.00	0.00	0.00	0.98	0.02

Table 3

Origin identification performance when the sample consists of 40 individuals from the Iijoki River (Ii) and 10 individuals from another stock. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.Baseline information was in each case available only from Ii (40 simulated individuals). The numbers are based on 50 replicates of each configuration.

Stock without baseline (outgroup)	Percentage of correct recognition for individuals from Ii			Percentage of correct recognition for individuals from the outgroup			Percentage of replicates where at least 50% of the outgroup was recognized
	min.	max.	avg.	min.	max.	avg.	
Neva	0.95	1.00	0.9955	0.9	1.00	0.998	1.00
Oulu	0.875	1.00	0.9665	0.0	1.00	0.7440	0.86
Simo	0.85	1.00	0.9705	0.0	1.00	0.6820	0.90
TornW	0.90	1.00	0.9820	0.0	0.80	0.3660	0.34

categorized in this respect as neutral (no biasing effect; Table 4, A and B), positive (strengthens the inference; Table 4C), negative (biases the inference; Table 4, D and E).

Our results indicate that commonly occurring levels (<5%) of missing marker data do not inhibit the ability of our method to detect the correct stocks, assuming that the missing values are randomly distributed over loci and individuals (Table 5). As an overall conclusion from the simulations, it is clear that the genetic dissimilarities of the stocks matter most for identification performance. When baseline samples are available for all stocks, most individuals can be correctly assigned to their origin even when the genetic distance between the stocks is negligible (such as between Tornionjoki and Iijoki rivers). Usefulness of the conditional posterior probabilities for characterization of the allocation uncertainty is exemplified in Table 6.

The number of inferred putative stocks was in general well in accordance with the underlying true number and there was no tendency to overestimate k. However, when the number of available marker loci was decreased to five (Table 7), the probability of obtaining additional putative stocks was slightly increased. Because it is widely known that the level of polymorphism of the markers affects their usefulness in origin identification, it is difficult to specify very clear boundaries with respect to the amount of loci necessary for an acceptable performance of any assignment method. It is important to notice that an acceptable characterization of uncertainty inherently depends on the real biological context in a particular modeling situation. As a simple rule of thumb for our method, we would suggest that $N_L \leq 6$ might be regarded as an insufficient value for reliable estimation. However, when auxiliary information is available such that the sample data can be grouped before analysis (as in Table 8), the statistical power to detect correct origins and k increases considerably. This situation would correspond to a geographical sampling scheme where the individuals assigned to the same sampling unit are caught simultaneously at a specific location.

Discussion

We have introduced a novel Bayesian method for an investigation of stock mixtures using molecular marker data by suitably modifying existing partition-based Bayesian models for estimation of genetic population structure. To enable smooth applicability, the implementation is made freely available in a user-friendly software. One particular advantage of our method is the possibility of appropriately analyzing data in a situation where only partial baseline information is available for the potential stocks. Use of an analytical integration approach enhances considerably the numerical performance when the stock mixture structure is challenging (e.g., in the presence of small stocks for which no baseline samples have been collected).

Contrary to the earlier Bayesian methods introduced in Corander et al. (2003, 2004), we have exploited a considerably less computationally intensive strategy that is based on stochastic optimization instead of MCMC simulation. To obtain stable estimates for moderate to large data sets, many long parallel MCMC chains would be needed, but the process for obtaining these chains often is not feasible under a single CPU architecture. Our intelligent search strategy, instead of the random search used in MCMC, seems to resolve this problem very efficiently. A disadvantage of stochastic optimization compared to optimization with MCMC is that a statistically consistent estimate of the number of stocks contributing to the sample cannot be derived. Nevertheless, our novel method has performed satisfactorily in this respect under realistic sampling scenarios. We are currently exploring possibilities for using intelligent proposals in MCMC and an online-based parallel implementation of the method, both of which would provide an ideal framework for biologists using molecular data in stock mixture estimation.

The most relevant biological assumptions used in our approach are HWE and nonlinkage of the marker loci. The latter assumption is generally valid, at least approximately, for the microsatellite markers often used in

Table 4

Allocation of 30 sample individuals from each of five stocks (150 individuals in total) under different baseline settings: (**A**) no baseline, (**B**) 40 baseline individuals from TornW, (**C**) 40 baseline individuals from TornW and Ii, (**D**) 15 baseline individuals from TornW and Ii, (**E**) 15 baseline individuals from Simo. Each "C" refers to an inferred putative stock for which no baseline information was available. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.

		Allocation				
Origin		C1	C2	C3	C4	C5
A	TornW	3	1	0	3	23
	Simo	1	1	0	25	3
	Ii	0	1	0	4	25
	Oulu	0	28	0	0	2
	Neva	0	1	29	0	0
		TornW	C2	C3	C4	
B	TornW	28	1	1	0	
	Simo	2	27	1	0	
	Ii	26	4	0	0	
	Oulu	2	0	28	0	
	Neva	0	0	0	30	
		TornW	Ii	C3	C4	C5
C	TornW	22	6	1	1	0
	Simo	1	2	26	1	0
	Ii	5	25	0	0	0
	Oulu	3	1	0	26	0
	Neva	0	0	0	0	30
		TornW	Ii	C3	C4	
D	TornW	24	5	0	1	
	Simo	1	2	0	27	
	Ii	5	23	0	2	
	Oulu	29	1	0	0	
	Neva	0	1	29	0	
		Simo	C2	C3	C4	C5
E	TornW	12	2	1	15	0
	Simo	29	1	0	0	0
	Ii	24	0	0	5	1
	Oulu	1	0	28	1	0
	Neva	0	0	0	0	30

Table 5

(**A**) Average numbers of allocations (over 20 replicates) to the different stocks under an uneven sample size distribution: TornW, n=60, Simo, n=20, Ii, n=30, Oulu, n=5, Neva, n=10. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The number of baseline individuals available from each of the five stocks was 30. The column with the heading "Other" refers to additional stocks inferred by the method. The results in (**B**) are otherwise based on an analogous configuration, except that 5% of the marker data was randomly set as missing values.

		Allocation					
Origin		TornW	Simo	Ii	Oulu	Neva	Other
A	TornW	47.5	1.2	7.9	3.2	0.0	0.3
	Simo	0.6	18.9	0.3	0.2	0.1	0.0
	Ii	3.1	1.2	25.3	0.5	0.0	0.0
	Oulu	0.3	0.0	0.1	4.7	0.0	0.0
	Neva	0.0	0.1	0.1	0.0	9.9	0.0
B	TornW	47.4	1.7	7.2	3.6	0.2	0.2
	Simo	0.6	18.4	0.8	0.3	0.0	0.1
	Ii	3.5	1.1	25.0	0.5	0.0	0.1
	Oulu	0.3	0.1	0.1	4.6	0.0	0.0
	Neva	0.0	0.1	0.0	0.1	9.9	0.1

Table 6

Average conditional posterior probabilities (over 20 replicates) for allocations of individuals to the different stocks under an uneven sample size distribution: TornW, n=60, Simo, n=20, Ii, n=30, Oulu, n=5, Neva, n=10. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The number of baseline individuals available from each stock was 30. The column with the heading Other refers to additional stocks inferred by the method.

	Allocation					
Origin	TornW	Simo	Ii	Oulu	Neva	Other
TornW	0.80	0.03	0.13	0.04	0.00	0.00
Simo	0.02	0.94	0.03	0.01	0.00	0.00
Ii	0.12	0.04	0.82	0.03	0.00	0.00
Oulu	0.06	0.01	0.03	0.90	0.00	0.00
Neva	0.00	0.00	0.00	0.01	0.99	0.00

stock mixture analyses. Minor deviations from HWE are not expected to notably affect our inference method; however, presence of samples from small stocks under strong inbreeding could result in an overestimation of k when there is limited baseline information available. Samples from such stocks would tend to be split into parts by the model if no baseline information about the stock allele frequencies can be used to identify the joint origin.

In addition to the molecular markers, auxiliary information, such as simultaneous catch at a common geo-

Table 7

Average numbers of allocations (over 20 replicates) to the different stocks under an uneven sample size distribution: TornW, n=60, Simo, n=20, Ii, n=30, Oulu, n=5, Neva, n=10. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The number of baseline individuals available from each of the five stocks was 30. The column with the heading "Other" refers to additional stocks inferred by the method. The marker loci used for inference were randomly sampled from the original nine microsatellites for each replicate; in (**A**) seven loci were used, in (**B**) five loci were used.

		Allocation					
Origin		TornW	Simo	Ii	Oulu	Neva	Other
A	TornW	44.5	3.2	7.6	4.3	0.2	0.0
	Simo	0.9	17.8	0.9	0.4	0.0	0.1
	Ii	2.8	1.6	24.7	0.9	0.1	0.0
	Oulu	0.3	0.1	0.2	4.5	0.0	0.0
	Neva	0.0	0.0	0.0	0.0	10.0	0.0
B	TornW	37.3	4.5	9.3	5.5	0.5	3.1
	Simo	1.0	16.5	1.4	0.6	0.2	0.4
	Ii	3.3	2.8	21.2	2.2	0.1	0.5
	Oulu	0.5	0.2	0.4	4.0	0.0	0.1
	Neva	0.1	0.0	0.1	0.2	9.6	0.2

graphical location, can be incorporated into the analysis. This information is incorporated by the pre-assignment of individuals in the catch data to *a priori* sampling units, when such are considered to be relevant for the species under investigation. Such prior information is particularly useful if the available molecular data are scarce because it enhances the statistical power to detect correct stock origins, as illustrated in our example analyses.

Although the Bayesian method that we propose seems to be a versatile tool for stock mixture identification, certain modifications of the model would also provide fruitful extensions for a variety of biological settings. Current use of the auxiliary information necessitates that the individuals assigned to the same sampling unit represent with certainty the same origin. However, the existence of such conclusive information cannot be assumed in applications in general. There is still a possibility of incorporating information about a tendency to a geographical clustering among the catch individuals with respect to the stock origin, through a suitable modification of the prior distribution of the partitions. In general, use of biological information concerning the behaviour of a species, in combination with geographical sampling information, provides a rich area for further model development. In particular, this combination of information highlights the potential use of the Bayesian statistical framework because the relevant biological information can often be efficiently incorporated through the prior distributions for the model parameters.

Table 8

Allocation of the 25 sample individuals from each of five stocks (125 individuals in total) under different baseline settings: (**A**) no baseline, (**B**) 15 baseline individuals from each stock, (**C**) 15 baseline individuals from each stock, and auxiliary biological information was introduced by considering the simulated catch data as sampling units of the size of five individuals. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. Each "C" refers to an inferred putative stock for which no baseline information was available.

		Allocation				
Origin		C1	C2	C3	C4	
A	TornW	20	0	4	1	
	Simo	2	0	2	21	
	Ii	20	1	3	1	
	Oulu	1	0	24	0	
	Neva	0	24	1	0	
		TornW	Simo	Ii	Oulu	Neva
B	TornW	18	0	7	0	0
	Simo	2	23	0	0	0
	Ii	0	1	23	1	0
	Oulu	2	0	0	23	0
	Neva	0	0	0	1	24
		TornW	Simo	Ii	Oulu	Neva
C	TornW	25	0	0	0	0
	Simo	0	25	0	0	0
	Ii	0	0	25	0	0
	Oulu	0	0	0	25	0
	Neva	0	0	0	0	25

Acknowledgments

The authors thank Marja-Liisa Koljonen for providing data about the microsatellite allele frequencies in Baltic salmon stocks. This work was supported by the Centre of Population Genetic Analyses, University of Oulu, Finland (Academy of Finland, grant no. 53297), and by Research funds of University of Helsinki, Finland.

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The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries

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Abstract—Bluefish (*Pomatomus saltatrix*) were tagged and released in Atlantic coastal areas between Massachusetts and Florida from 1963 through 2003 as part of a National Marine Fisheries Service (NMFS) project and a volunteer program sponsored by the American Littoral Society (ALS). A total of 15,699 bluefish were tagged by NMFS and 20,398 by ALS volunteers and 4.3% (1075 NMFS tags and 464 ALS tags) were recaptured and reported. Time-at-large was limited; 65.8% of the recaptured tags were returned within two months of tagging, although nineteen of the returned tags remained at large for two years or more. Tag returns indicated seasonal migrations of fish between the Middle Atlantic Bight and Florida. Three groups of bluefish are proposed for Atlantic coastal waters on the basis of tag return data and are defined by the seasonal occurrence of fish between 30 and 45 cm fork length. The northern group occupied the area from Massachusetts to Delaware between late spring and late fall. Bluefish in the central region between Maryland and North Carolina represented a combination of seasonal transient and resident fish, as did the southern group in Florida. Mixing occurs among all three groups; and larger fish (>45 cm) spend winters in offshore areas. Estimates of von Bertalanffy growth parameters from tagging data were comparable to scale-based estimates. Swimming speeds between point of release and recapture averaged 2.6 km per day, and seasonal spikes greater than 5 km per day corresponded with periods of migration in spring and autumn.

Manuscript submitted 9 May 2005
to the Scientific Editor's Office.
Manuscript approved for publication
19 December 2005 by the Scientific Editor.
Fish. Bull. 104:559–570 (2006).

Bluefish (*Pomatomus saltatrix*) is a pelagic species with a worldwide distribution in temperate and subtropical oceans. In the United States, bluefish are found along the Atlantic coast from southern Florida to Cape Cod, Massachusetts, and occasionally as far north as Nova Scotia (Collette and Klein-MacPhee, 2002). The broad-scale seasonal movements of bluefish are known within the commercial and recreational fishing communities (Hersey, 1987), but details of the migratory pattern remain poorly documented in the scientific literature. Tagging studies provide the most direct evidence of seasonal movements, but the only published account for the Atlantic coast stock is a study in Long Island Sound by Lund and Maltezos (1970). Wilk (1977) provided a description of bluefish migration that remains the accepted standard and which was based on seasonal distribution of commercial and recreational catches, as well as on unpublished results of a tagging project conducted during the 1960s by David Deuel and colleagues at the NMFS James. J. Howard Marine Sciences Laboratory (formerly known as the Sandy Hook Marine Laboratory). The proposed migration involved a north–south coastal movement between New York–New Jersey offshore waters and southeastern Florida offshore waters during the fall and a return spring migration along the same route. Larger fish (i.e. greater than three pounds) were believed to follow a more offshore pathway.

The identification of distinct bluefish stocks contributing to this migratory group has been the subject of multiple investigations. The racial composition of bluefish on the Atlantic coast was investigated by Lund (1961) who concluded, primarily from differences in the number of gill rakers of small bluefish, that six races existed along the coast. Lassiter (1962) found differences in first year growth on scales, which indicated that two groups of fish inhabited North Carolina waters. Returned tags from bluefish tagged in the Long Island area

(Lund and Maltezos, 1970) also indicated two distinct stocks, although not necessarily the same groups as defined by Lassiter (1962). More recently, some scientists have concluded that either two distinct spawning groups exist (Norcross et al., 1974; Kendall and Walford, 1979) or one stock with two distinct survival periods (Hare and Cowen, 1993; Smith et al., 1994). Others, probing mitochondrial DNA (mtDNA) (Graves et al., 1993), have concluded that Atlantic coast bluefish constitute a single population. A discriminant function analysis of morphometric data has corroborated the one stock hypothesis despite evidence of phenotypically plastic characteristics (Austin et al., 1999).

Mark-recapture experiments provide an empirical method for evaluating both migratory behavior and stock composition. In 1962, the National Marine Fisheries Service (NMFS) initiated a study of the migratory patterns of bluefish to obtain information on the population structure of the Atlantic coast stock; this coastwide tagging program continued until 1967. The American Littoral Society (ALS) also coordinates an annual tagging program by private citizens that has resulted in 20 years of tag releases for a variety of species, including bluefish. This combined tag-recapture information constitutes the largest known tagging database for this species. The goal of our study was to investigate the migratory behavior of bluefish along the Atlantic coast by using the results of these previously unpublished tagging studies and to examine the single stock hypothesis in context of tag recovery information.

Materials and methods

The NMFS bluefish tagging program used several types of tags (variously colored). Field tests in 1963 indicated that a dorsal loop spaghetti tag would be more suitable, owing to a longer retention rate, than dart tags or jaw tags. This loop tag, described by Watson (1963), was closed with a pressure-fitted V-shaped clip. In addition, two other types of dorsal loop tags (both closed by knotting the ends of the tubing, and one having a clear outer covering) and an internal anchor tag (5/16 by 1-1/4 inches, with a 3″ streamer as described by Topp [1963]) were used. For visibility of the tags to fishermen, orange was chosen as the color for most of the dorsal loop tags and yellow for the streamer of the internal anchor tags. The fork length of each fish tagged and released was measured to the nearest cm. Recapture information was mailed to NMFS in Sandy Hook, NJ, and included data on recapture location, recapture date, fish length (usually in inches), and weight (lbs and oz, when possible).

The ALS program uses yellow dorsal loop tags that are inserted with a hollow needle through the muscle below the dorsal fins and tied with a simple overhand knot or, as in some recent tags, fastened with a snap-lock mechanism (Carlsen, 2000). Details on the date, location of release, fork length (to the nearest inch), and weight (lbs and oz, when possible) were furnished by the fishermen at the time of release. Information regarding tag recapture (including location, recapture date, fish length [inch] and weight) was mailed to ALS headquarters by the fishermen and the distance of the recapture location from shore was coded as inland, inshore (≤3 miles), or offshore (>3 miles). Not all tags recaptured in the ALS program were reported with complete details. As a result, some of the sample sizes presented in the present study differ among analyses, depending on the available data of the recaptured tags. Also, in order to standardize data from both programs and to minimize precision error resulting from unit conversions, fish length data are presented in centimeters followed by the inch equivalent rounded to the nearest whole number.

Several types of fishing gear were used to capture bluefish in the NMFS tagging program. Fish were captured by using gill nets deployed from research vessels, hook and line, commercially operated pound nets, and beach seines; bluefish tagged in the ALS program were captured with hook and line.

Bluefish tagged in the NMFS program were released in areas of seasonal abundance from southeastern Florida to Massachusetts, and major tagging efforts were made in southern Florida, North Carolina, Virginia, New Jersey, and New York (Fig.1). ALS tag releases were concentrated in the New York–New Jersey area, although tagging occurred from Florida to New England (Fig.1). Each ALS recapture location was categorized into 1 of 59 geographic areas and was assigned a latitude and longitude based on the center point of the recapture area. NMFS recaptures were assigned latitude and longitude coordinates based directly on recapture location.

Distance (km) traveled was calculated as the great circle distance between the point of release and point of recapture (NMML[1]) and there was a suitable waypoint if the pathway traversed land. Swimming speed was calculated as the linear distance traveled divided by days at large. In order to allow for acclimation to the presence of the tag, fish recovered within the first three days of release were not included in analyses. Additionally, because speed calculations were influenced by the number of days at large, speed estimates per two-month increments were restricted to tags recovered within 30-day periods to minimize recoveries spanning several months and to avoid averaging speed over various migratory phases. Swimming speeds were compared among months by using an analysis of variance (ANOVA) (Zar, 1974). Comparison of movements by size was made for 5-cm length classes to reduce potential bias from measurement error of recaptured fish.

Bluefish growth was modeled by using the change in fork length during the time-at-large. Von Bertalanffy growth curve parameters L_∞ and K were calculated by using the Fabens model (Fabens, 1965):

[1] NMML (National Marine Mammal Laboratory). 2004. Excel geometry functions. Website: http://nmml.afsc.noaa.gov/Software/ExcelGeoFunctions/excelgeofunc.htm [accessed 4 October 2004].

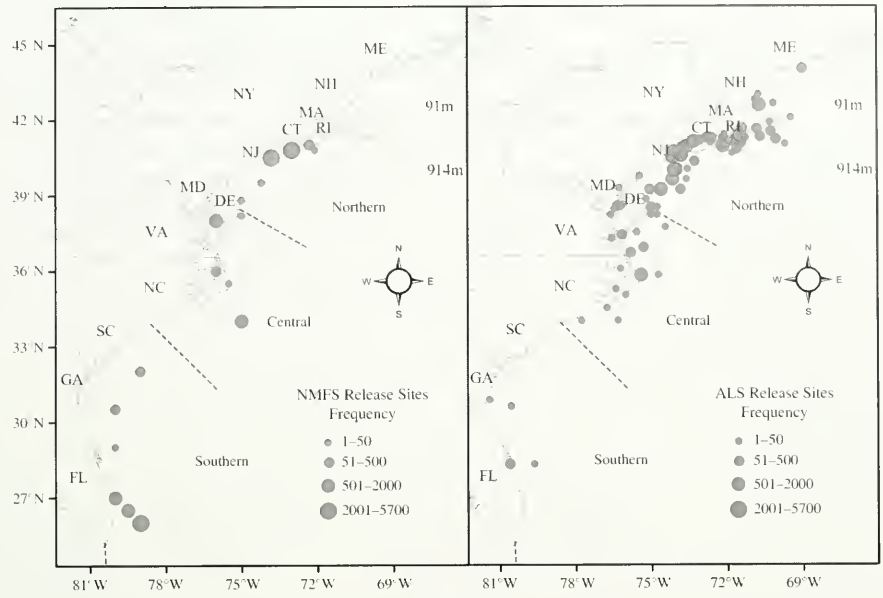

Figure 1

Distribution of release sites (by region) for bluefish (*Pomatomus saltatrix*) released during National Marine Fisheries Service (NMFS) (1963–1967) and American Littoral Society (ALS) (1983–2003) tagging programs.

$$L_{r,i} = L_{t,i} + (L_\infty - L_{t,i})(1 - e^{-K\Delta t_i}),$$

where $L_{r,i}$ = length at time of recapture;
$L_{t,i}$ = length at time of release; and
Δt_i = change in time (years) between release and recapture.

Parameter estimates were derived by using the SAS NONLIN procedure (SAS Inst., Inc., Cary NC). ALS and NMFS data were modeled separately because of a difference in the resolution of size measurements at release (centimeters for NMFS and inches for ALS). Bluefish at large less than 14 days, or fish with zero or negative growth, were excluded from the calculations.

Geographic distributions for tag recoveries were compared with commercial catch locations of bluefish reported from the Middle Atlantic Bight. NMFS vessel logbooks from commercial fishermen in the Northeast region contain information about landings, discards, and the spatial location of catch. Bluefish catch locations from 2001 to 2003 were summarized by month for all gear types. Length samples (measured to the nearest cm) collected by NMFS port agents from commercial landings were expanded to represent length distributions of total reported landings.

Results

During 1963 to 1967, the NMFS bluefish project tagged and released 15,699 bluefish; of these, 11,624 fish (74.0%) were captured with gill nets, 1393 (8.8%) with hook and line, 907 (5.8%) from beach seines, and 1775 (11.3%) from pound nets. Included in the hook-and-line total were 224 fish tagged by volunteer sportsmen in south Florida, New Jersey and New York (which resulted in 17 recaptures). The number of bluefish tagged and released are summarized by month and area in Table 1. From 1983 to 2003, recreational hook-and-line fishermen in the ALS tagging program caught and released 20,398 bluefish. Later recaptures totaled 1539 fish, of which 1075 were NMFS tagged and 464 were ALS tagged.

The NMFS rate of tag return varied by capture method, tag type, and tagging area. The highest return rates (9.6 %) were from pound net releases that could be attributed, in part, to a high recapture rate immediately after tagging. The second highest percentage (6.9 %) and largest number of recaptures (802) were fish captured with gillnets. Although only 4.7% of the fish released from hook-and-line gear were returned, over half of these released fish were from the first year of the tagging program (775 fish tagged, 16 returned, 2.1%),

Table 1

Number of bluefish (*Pomatomus saltatrix*) tags released by month and location of National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) programs.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
NMFS														
North	New England								4	26				30
	New York						196	31	1082	1859	150			3318
	north New Jersey						614	614	2651	1811				5690
	south New Jersey						3	1	4					
Central	Maryland						20							20
	Virginia					964	4							968
	North Carolina					127	274	40	57	43	569			1110
South	South Carolina				60	19								79
	north Florida				335	335								
	south Florida	510	572	1199	1008						100	425	331	4145
	Total	510	572	1199	1403	1110	1111	686	3794	3739	819	425	331	15,699
ALS														
North	New England	1	1		3	124	846	1233	1470	1845	1410	440	1	7374
	New York				3	368	803	568	568	661	1143	323	2	4439
	north New Jersey				76	1383	1181	814	956	961	837	411	22	6641
	south New Jersey					4	90	18	18	25	26	11		192
Central	Maryland					35	66	21	35	32	63	5	2	259
	Virginia				8	153	122	8	6	3	5	18	14	337
	North Carolina				11	21	6	4	14	10	421	124	26	637
South	South Carolina													
	Georgia				7	2		1	3	2	2	1		18
	Florida	122	43	59	93	24	1	5	2	9	23	20	100	501
	Total	123	44	59	201	2114	3115	2672	3072	3548	3930	1353	167	20,398

whereas the remainder of the hook-and-line releases (618 fish) resulted in 49 recaptured fish (7.9%). This difference may be attributable to less effective tags used during 1963, rather than the capture method. All ALS releases were fish caught with hook and line, but gear type was not recorded for the recaptured fish.

Tag types differed in rates of return and in time fish spent at large. Return rates for NMFS tags were similar between dorsal loop tags (760 of 10,752; 7.1%) and internal anchor tags (310 of 4441; 7.0%). All NMFS tagged fish recaptured after 17 months at liberty had been tagged with internal anchor tags. Abrasion of some dorsal tags occurred after two months and appeared more severe on tags returned from Florida releases. Some abrasion occurred on the external streamer of the internal anchor tags. ALS dorsal loop tags resulted in an overall return rate of 2.2%.

Return rates for the NMFS tags varied by area, from 4.5% in New York to 10.2% from Florida (Table 2). Eighty-three percent of recaptured tags that were at liberty one year (n=24) were from tagging in areas north of New Jersey, and all recaptured tags at liberty 2, 3, and 4 years (10, 4, and 4 fish recaptured, respectively) were also from tagging in these areas (Table 2). For all areas combined, 51.3% of the NMFS recaptured fish were at liberty less than one month and 88.1% were at liberty less than five months. Among ALS tags, 50.3% were at liberty for two months and 79.3% for five months or less. Only 4.5% of all returned fish were at liberty greater than one year and 1.2% greater than two years. The longest time-at-large for an ALS tagged bluefish was 1461 days and 1486 days for a NMFS-tagged fish.

The size at release of the 36,097 tagged bluefish differed between the two programs. Fork lengths (FL) ranged from 19 to 57 cm (7 to 22 inch) for NMFS and 15 to 114 cm (6 to 45 inch) for ALS (Fig. 2). The majority of fish released in the NMFS program (83.1%) were 30 to 45 cm (12 to 18 inch) and were 1-, 2-, or 3-year-olds according to estimates determined from scales from a subsample of similar size fish collected during the tagging operations. A greater size range of bluefish were tagged in the ALS program, and 88.2% measured 30 to 76 cm (12 to 30 inch).

Size frequencies of bluefish released, and of those subsequently recaptured, differed despite the relatively short times at large (Fig. 2). Changes in length can be attributed to growth, unit conversion, and associated measurement error. The NMFS recapture data set had 616 tag recoveries with appropriate fork length and time-at-large information, whereas the ALS set had 336 with these data (Fig. 3). The von Bertalanfy growth parameter estimates from these data were L_∞ of 100 cm and 118 cm (39 and 46 inch) for NMFS and

Table 2

Number of bluefish (*Pomatomus saltatrix*) tags returned from each release area by months at liberty. ALS = American Littoral Society; NMFS = National Marine Fisheries Service; NE = New England; NY = New York; NJ = New Jersey; MD = Maryland; VA = Virginia; NC = North Carolina; SC = South Carolina; FL = Florida.

	ALS							NMFS									
Month	NE	NY	NJ	MD	VA	NC	FL	NE	NY	NJ	VA	NC	SC	FL	ALS total	NMFS total	Combined total
0	20	48	40	3	3	2	9	1	36	178	34	37	2	265	125	552	677
1	32	30	38		1	2	3		30	68	9	17	2	102	106	229	335
2	20	27	24		4		3		5	32	7	6	1	43	78	94	172
3	7	15	14				3		7	10	4	4		22	39	47	86
4	5	5	6						3	4	6	2		10	16	25	41
5	3	3	1							4	3	3		4	7	14	21
6	2	1	1						4	1		1		3	4	9	13
7	3	7	1		1					1	2				12	3	15
8	4	12	2						3	3		1		1	18	8	26
9	1	6							8	3				1	7	12	19
10	4	5	4						13	4		1			13	18	31
11	1	5	2						12	6	1			2	8	21	29
12	1	5	3		1				6			1		1	10	8	18
13	2	3							6	3				1	5	10	15
14	1		1						1	2					2	3	5
15		1													1	0	1
16		1									1				1	1	2
17											1				0	1	1
18															0	0	0
19														1	0	1	1
20									1						0	1	1
21															0	0	0
22	2								1						2	1	3
23	1								3						0	3	3
24									3						1	3	4
25+	3	1						1	7	3					4	11	15
No. recaptured	112	175	137	3	10	4	18	2	149	322	68	73	5	456	459	1075	1534
No. released	7374	4439	6833	259	337	637	519	30	3318	5694	968	1110	79	4480	20,398	15,699	36,097
Return rate	2%	4%	2%	1%	3%	1%	3%	7%	4%	6%	7%	7%	6%	10%	2%	7%	4%

ALS, respectively, and K values of 0.230 and 0.206, respectively. The 95% confidence interval around L_∞ for the NMFS data ranged from 79 to 121 cm (31 to 48 inch) and ALS estimates ranged from 95 to 141 cm (37 to 56 inch). Confidence intervals for the K parameter ranged from 0.135 to 0.324 for the NMFS data and 0.109 to 0.303 for the ALS data.

A single vector drawn between tag release and recapture locations represents the shortest possible water route traveled between the two points. The actual route of travel likely diverts from this path; however it remains the basis for determining distance traveled. Movement of bluefish between western Long Island Sound and lower New York Bay through the East River was not indicated by the tag return data, and therefore passage of bluefish through the East River was not considered in the distance calculations. Seventy-five percent of the NMFS tags were recaptured within 100 km of the tagging location; whereas 9.7% were caught 350 km or farther from the tagging area. The maximum distance traveled was 2227 km (Chesapeake Bay to west Florida) for a fish at liberty 341 days (6.5 km per day). For the ALS recaptured fish, 59.7% were recaptured within 100 km of the point of release and 40.3% (187) traveled beyond 100 km averaging 295 km, and 45 bluefish traveled more than 400 km. The maximum distance was 1096 km for a fish at liberty for 76 days (14.4 km/day).

The number of days at liberty represents the maximum time possible for a fish to travel the straight-line distance between the tagging and recapture locations. Movement was generally less than 5 km per day (84.3% of recaptures) and the overall average speed of fish recaptured in both programs was 2.6 km per day. Seventeen bluefish traveled more than 20 km per day and had a maximum swimming speed of 48.3 km per day for three days.

The average swimming speeds for combined NMFS and ALS recaptured fish were significantly different among months (P=0.02). Speeds were highest during the autumn, peaking during October–November at 5.3 km per day, and there was another spike during April–May at 4.9 km per day (Fig. 4). These seasonal peaks were in contrast to the overall average of 2.6 km per day. Seasonal variations in swimming speed were considered indicative of periods of active migratory behavior. This annual cycle of movement was divided into four periods based on the average rate of travel for each month: winter residency (December to February), spring migration (March to May), summer residency (June to August), and autumn migration (September to November).

The swimming speed and distance traveled during seasonal movements were different for all bluefish size groups. Swimming speed of fish 30–45 cm (12–18 inch) was greater than speed of fish 45–65 cm (18–26 inch) and this pattern was consistent across regions (Fig. 5). The speed disparity by size was influenced by the distance traveled, not by differences in time-at-large because the data were limited to recoveries within 90 days. Smaller bluefish, particularly those released in the northern region, traveled farther distances on average than fish in the larger size classes (Fig. 5).

Movement of tagged fish among areas is a function of both the behavior of the animal and adequate time-at-large to exercise that behavior. Half (229 of 459 fish with location information) of bluefish tagged with ALS tags were recaptured beyond the state of release; the remaining recaptured fish were caught in the area of release (Table 3). NMFS releases had a higher proportion recaptured bluefish within the state of release (77.1%; Table 3). Most long distance returns occurred during the first year after tagging; recoveries in years 1 through 4 after tagging were generally from the area of release (62 of 100) or in the release area and adjacent areas (91 of 100). Fish recaptured from New Jersey northward accounted for 89 of the 100 recaptured

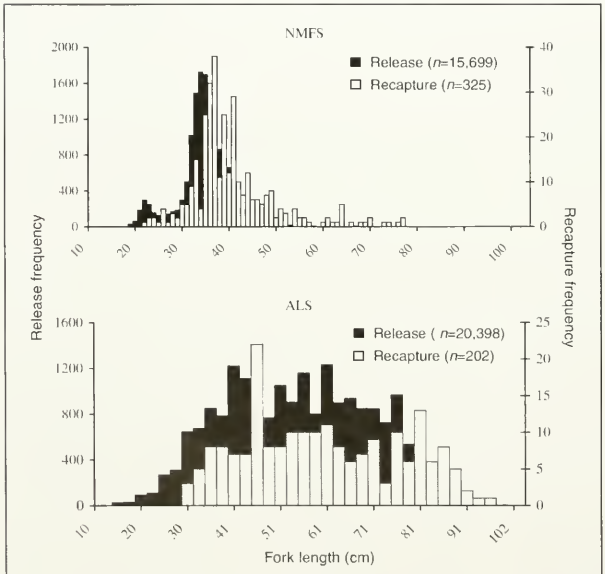

Figure 2

Frequency distributions for release and recapture fork lengths of bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) tagging programs.

fish after one year at liberty, and all but two of these were from releases in this area. The higher percentage of recaptured fish from Florida may reflect greater annual fishing effort in contrast to northern areas.

Seasonal recaptures of tagged bluefish along the coast (Fig. 6) were a function of both fishing effort and the abundance of tagged fish in the area. Over ninety-one percent of all recaptured NMFS fish (978 of 1,075) were caught in inshore areas (including Chesapeake Bay, Delaware Bay, and Long Island Sound) or within one mile of the coast. Of the remaining 99 recaptures: one fish was caught 75 miles offshore and the rest within 30 miles of the coast; 47 between 1 and 6 miles, 40 between 6 and 20 miles, and 9 between 20 and 30 miles. Tagged fish released in New York and New Jersey accounted for 45 of the 50 returns over 6 miles offshore; 4 of those remaining fish were both released and recaptured off Florida, and the last fish had been released in Florida and recaptured off New Jersey. All of these 45 returns released from New York and New Jersey were recovered north of Delaware—most off New Jersey and New York. The offshore returns occurred from May through November, although most of the fall recaptured fish had been released during the same season (21 of the 23 recaptures in September, October, and November), whereas most spring and summer recaptured fish had been at liberty for at least one year (19 of the 22 recaptures from May though July).

Seasonal patterns of bluefish migration, determined from information within recovered tags, generally followed one of three patterns: north–south between the northern Middle-Atlantic and Florida; a north–south pattern within the Middle-Atlantic; and year round movements between inshore and offshore Florida. To simplify examination of migration patterns, recapture locations were divided into three regions. The area from Delaware to New England was designated the northern region, Maryland through North Carolina as the central region, and the area between South Carolina and southern Florida as the southern region. The single fish recovered in western Florida was ignored for our analysis. A recovery matrix by region showed that greater than 90% of the bluefish recaptured within the northern or southern region had originated within the same region (Table 4). However, within the central region, the percentage of recaptured fish originating in that region was only 80.3%. The remaining tags were either recaptured to the north (12.7%) or the south (7.0%). Distribution maps

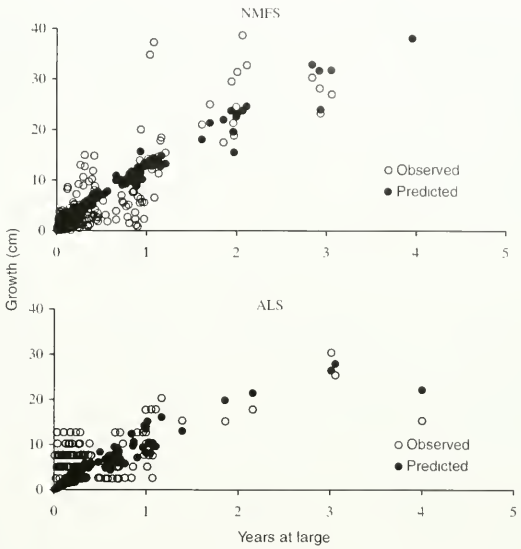

Figure 3

Changes (observed and predicted) in fork length during time at large (years) for bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) tagging programs.

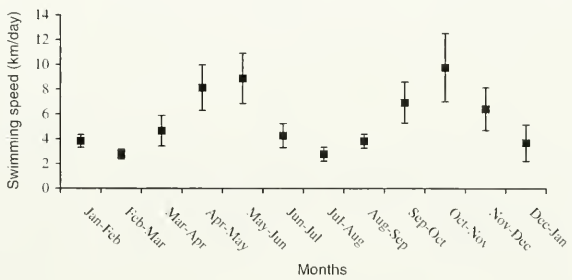

Figure 4

Mean monthly swimming speeds (km/day) of bluefish (*Pomatomus saltatrix*) ±95% confidence intervals from two combined program tag recoveries: National Marine Fisheries Service (1963–1967) and American Littoral Society (1983–2003).

of seasonal recaptured fish (Fig. 6) further highlighted the pattern of a northerly migration that began in May and was followed by southerly migration beginning in December. However, the entire coastal stock did not make the seasonal shift. Bluefish released in southern Florida were recaptured locally during the summer residency period and other fish tagged in southern Florida appeared in coastal New Jersey (Table 3).

Seasonal distribution data from bluefish tag returns indicated a southward movement of fish during the fall, culminating in an over-wintering aggregation near Cape Hatteras, North Carolina, and to the south. Commercial catch records from the Middle Atlantic for 2001 to 2003 indicated a greater seasonal inshore-offshore movement than that implied from tag recoveries. Vessel logbook data indicated that bluefish are present in the northern and central areas throughout the winter and have an increasingly offshore and southern distribution as water temperatures decrease. By March, the commercial catches increase off the coasts of Virginia and North Carolina (Fig. 7). The sizes of fish in these commercial catches were generally larger than those of tagged fish; lengths were between 25 and 70 cm and mean size was 45 cm. The commercial catch distribution expanded northward beginning in April, in a direction similar to the bluefish migratory route indicated by spring tag returns.

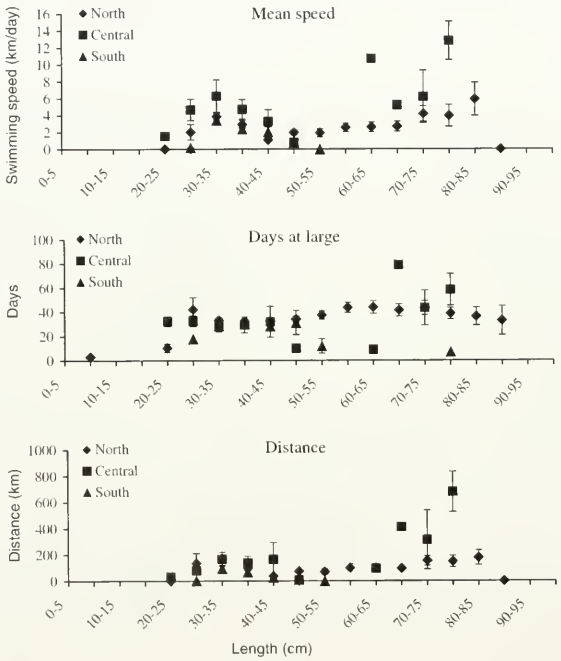

Figure 5

Mean swimming speed, days at large, and distance traveled (±95% confidence interval) by length for bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service and American Littoral Society tagging programs.

Discussion

A generally established hypothesis for bluefish migration is that fish undergo a seasonal coastal migration, leaving the Mid-Atlantic Bight in autumn as water temperatures decrease and moving as far south as Florida. In spring, bluefish return north where they spend the warmer months in habitat suitable for larger, mature fish—possibly in habitat extending across the continental shelf (Wilk, 1977; Fahay et al., 1999). Our hypothesis expands that migration pattern to suggest there are three bodies of fish with different migration behaviors. One group has an extensive north–south migration between New England and Florida, a second group has a migration route within the Mid-Atlantic Bight bounded to the south by North Carolina, and a third group has an inshore-offshore migration within Florida waters. The geographic ranges of these three groups overlap during at least part of the year and the seasonal areas of distributions change with fish size.

Bluefish from Massachusetts to Delaware (northern region) leave the coastal areas in autumn, and fish less than approximately 45 cm (18 inch) migrate south along the coast and are found in the south Florida winter fishery. However, tag return data indicate that part of this size group, as well as all fish over 45 cm (18 inch), move offshore in autumn and are distributed during winter in offshore areas south of Virginia. Both size groups return to the northern area in spring and summer a year after tagging, as well as in successive years.

The Mid-Atlantic area from Maryland to North Carolina (central region) appears to be a transitional area in the migratory route. A group of fish tagged in the northern region migrated in fall to the central region and remained throughout the winter, whereas other fish continued south to Florida. In the spring, a portion of the Florida fish moved back to the central region, while others continued through to the northern region. The distribution of commercial catches reported in logbooks confirmed the movement of bluefish into offshore waters during autumn, and movement increasingly south as winter progresses. The reported landings of large

Table 3

Recapture matrix by state of release for National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) bluefish (*Pomatomus saltatrix*) tag recoveries. NE = New England; NY = New York; NJ = New Jersey; DE/ME = Maine; MD = Maryland; VA = Virginia; NC = North Carolina; SC = South Carolina; FL = Florida.

NMFS	Recapture area										
Release area	NE	NY	north NJ	south NJ	DE/MD	VA	NC	SC	north FL	south FL	west FL
New England		2									
NY	2	96	33	4	1		3		3	7	
north NJ	2	25	210	31	8	2	32		6	6	
south NJ											
DE/MD											
VA			4	1	1	53	5	1		2	1
NC		2	3	1	4	56			5	2	
SC		1	4								
north FL									37		
south FL			3	2	1				36	377	

ALS	Recapture area										
Release area	ME	MA	RI	CT	NY	NJ	DE	MD	VA	NC	FL
AL											
ME		1									
MA		12	3	5		9	1	2	1	3	
RI		8	20	22	16	5		1		4	
CT		5	2	20	18	1	1			1	
NY		7	2	16	82	17	3			3	
NJ		3	3	13	25	65	10	4	2	5	
DE					1		4		1	1	
MD								3			
VA	1	1	1	2	1	2		1		1	
NC										4	
FL											19

bluefish fish during the Virginia–North Carolina winter fishery and the paucity of bluefish over 45 cm (18 inch) in the Florida fishery indicate that the larger fish do not continue the southern migration beyond North Carolina.

Bluefish are found throughout the summer in southern Florida (southern region) as evidenced by tag returns and fishery landings, although at a low level of abundance compared with fall through spring landings. The one fall recaptured tag in New Jersey from a fish released in Florida in the spring (at liberty 17 months) indicates that fish from the southern group are found in northern areas in subsequent years. Bluefish found off Georgia and South Carolina appear to be transitory, and are present primarily in spring and fall. The relative lack of tag recoveries in coastal South Carolina and Georgia implies a migratory pathway farther offshore, possibly closer to the shelf edge and Gulf Stream.

Change in fish size leads to a change in the seasonal migration route. The migratory groups are best defined

Table 4

Tag recovery matrix by region for combined National Marine Fisheries Service and American Littoral Society tags; data correspond to tag release and recaptures shown in Figure 6.

	Recapture region			
Release region	North	Central	South	Recaptures
North	812 (90%)	67 (7%)	22 (2%)	901
Central	20 (12%)	127 (80%)	11 (6%)	158
South	7 (1%)	4 (1%)	469 (98%)	480
Recaptures	839	198	502	1539

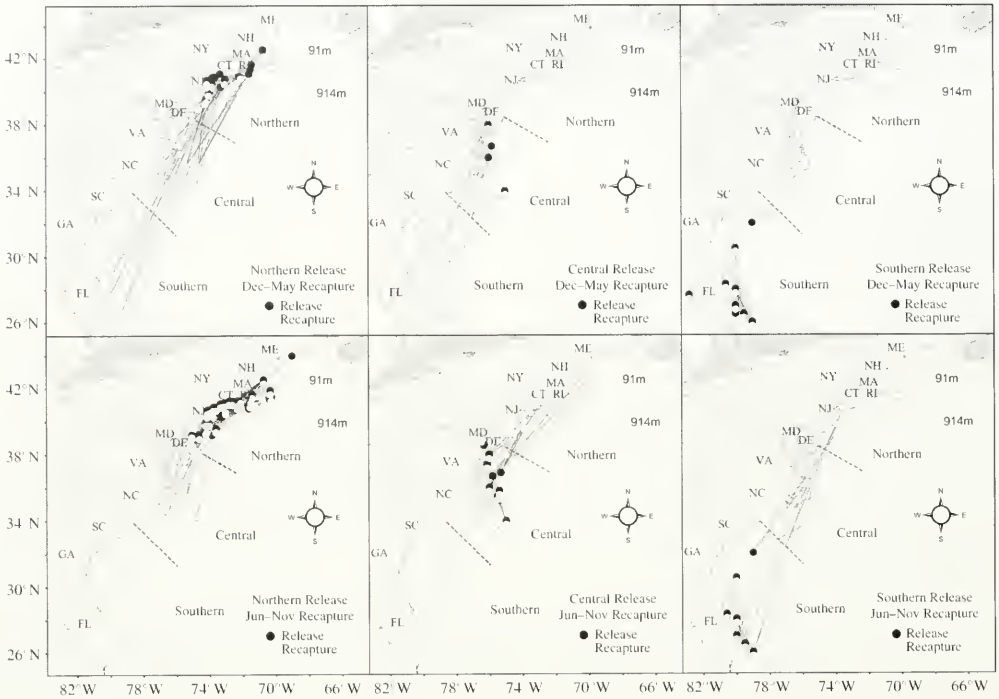

Figure 6

Geographic distribution of tag recoveries, by region of release and season of recapture, for bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) tagging programs combined.

by the seasonal aggregations of smaller fish (less than approximately 45 cm, 18 inch FL). Juvenile bluefish use a coastal migratory route that extends farther south and offshore with increasing size. Some fish past the juvenile stage may remain in Florida for a season while others return to northern areas in the first or second spring. As growth continues, north–south migration routes become truncated—replaced by a route that keeps fish within the Mid-Atlantic Bight circuit.

Because migration patterns appear to be size related, growth rate will determine how long individuals maintain a particular migration behavior. Tag-based growth rate estimates (K=0.23 and 0.21) are similar to values reported from scale-based age studies, but the tag model resulted in larger theoretical maximum sizes of 100 and 118 cm (39 to 46 inch). Salerno et al. (2001) reported an average L_∞ value of 87 cm and K equal to 0.26, whereas previously published estimates range from 67 to 128 cm (Lassiter, 1962; Wilk, 1977) and have K values ranging from 0.10 to 0.34 (Lassiter, 1962; Wilk 1977). The tag-based estimates of maximum size are similar in size to that of the largest fish reported in recreational landings (Salerno et al., 2001) and size of this largest fish caught in recreational landings could be considered an empirical estimate of L_∞. Otoliths have been shown to be preferable to scales for aging bluefish (Sipe and Chittenden, 2002). Growth parameters of bluefish from the South Atlantic, aged from otoliths (L_∞=101.9 cm, K=0.10 [Barger, 1990]), compare well with our tag-based estimates of L_∞, but produce very different growth-rate estimates.

The migration route bluefish follow from coastal New England to southern Florida, a distance of potentially >2000 km, is completed over the course of several months. Bluefish held in aquaria have been shown to travel at speeds from 40 to 60 cm/s and to have burst speeds up to 80–110 cm/s (Olla et al., 1970). An approximate average speed for bluefish similar in size to those tagged in the present study would be between 39 km per day (40 cm/s) and 59 km/day (60 cm/s). The majority of tagged fish moved between 0 and 5 km per day (84%), and most (97%) bluefish swam less than 20 km/day. However, several individuals averaged between 55 and 111 km per day. An average swimming speed

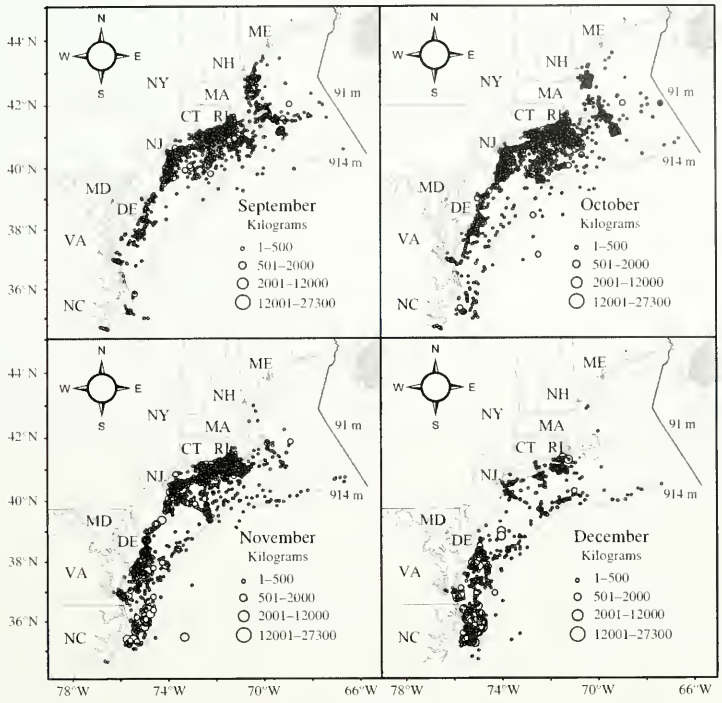

Figure 7

Distribution of bluefish (*Pomatomus saltatrix*) in the Middle Atlantic Bight based on commercial logbook catch records (2001–2003) for all gear types.

greater than 50 km per day would imply that some type of passive transport supplemented active swimming movement. The offshore distribution of bluefish in the South Atlantic Bight during winter, as inferred from tags, may provide an opportunity for bluefish to use the Gulf Stream during the northern migration.

Several recent studies have evaluated the stock structure of bluefish along the Atlantic coast by using genetic material (Chiarella and Conover, 1990; Graves et al., 1993; Davidson, 2002) and morphometric characteristics (Austin et al., 1999). These studies have concluded that bluefish along the U.S. Atlantic coast comprise a single stock. The tag recovery information for bluefish illustrates differences in movement patterns among areas, but these groupings do not imply unique stock characteristics. Consequently, there is no evidence from the tag recovery information that refutes the single stock hypothesis.

Implementation of a well-designed tag and release program is critical for analytical evaluation of migration (Schwarz et al., 1993). Limitations associated with tag recovery must be accounted for in the design of an effective tagging program. Recovery of most tags is a function of fishing effort; therefore recaptured tags must be considered in the context of the fisheries that will provide the recoveries. Unknown variations in fisheries over the past four decades may have influenced the patterns of bluefish tag recoveries in the NMFS and ALS programs, ultimately influencing interpretation of the results. In addition, time-at-large for fish in both programs was generally less than one year which may be due to tag-induced mortality and tag loss (Henderson-Arzapalo et al., 1999). Bluefish tagged in Western Australia were generally at large for less than a year and experienced tag losses between 25% and 38% (Young et al., 1999). The NMFS and ALS programs demonstrate that tagging is a viable tool in analyses of bluefish populations, but it has limitations. Using the knowledge gained from these tagging programs, scientist may find that a renewed tagging effort incorporating recent technological advances will provide further insight into the migratory behavior of bluefish and, in particular, the behavior linked to environmental cues.

Acknowledgments

The NMFS tagging project was conducted by David Deuel and his colleagues of NOAA Fisheries, Sandy Hook, New Jersey. Although their results were not published before Dave's death in 1994, his initiative in tagging bluefish made this study possible, for which we are grateful. We would also like to thank the American Littoral Society volunteers for data collected through their tagging program, Kristy Webber for data entry help, helpful reviews from Steve Cadrin, Mark Terceiro, and Fred Serchuk, and Ken Able for his constant encouragement to publish our tagging results.

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Abstract—We evaluated light-based geolocation estimates from pop-up satellite tags in high latitudes because some of the largest fisheries in the world are in areas where this technique has not been assessed. Daily longitude and latitude were estimated by using two Wildlife Computers software programs: 1) Argos Message Processor (AMP), which summarizes light intensity data transmitted to satellites, and 2) Time Series Processor (TSP), which uses more detailed data obtained from retrieved tags. Three experiments were conducted in the northern Gulf of Alaska using tags placed on 1) Pacific halibut in outdoor aquaria, 2) a fixed mooring line at various depths and 3) wild Pacific halibut. TSP performed better than AMP because the percentage of days with geolocation estimates was greater and the mean error magnitude and bias were smaller for TSP and increased with depth for both programs; however, latitude errors were much greater than longitude errors at all depths. Light-based geolocation enabled us to discern basin-scale movements and showed that the Pacific halibut in our study remained within the Gulf of Alaska. We conclude that this technique provides a feasible method for inferring large-scale population structure for demersal fishes in high latitudes.

Evaluating light-based geolocation for estimating demersal fish movements in high latitudes

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Manuscript submitted 24 August 2005 to the Scientific Editor's Office.

Manuscript approved for publication 20 December 2005 by the Scientific Editor.

Fish. Bull. 104:571–578 (2006).

Demersal fishes at high latitudes support some of the most lucrative fisheries in the world. An example is the Pacific halibut (*Hippoglossus stenolepis*) fishery off Canada and the United States. Currently, the International Pacific Halibut Commission (IPHC) manages the Pacific halibut population as a single, panmictic stock from northern California through the eastern Bering Sea based on genetic (Grant et al., 1984; Bentzen et al., 1998) and tagging data (Skud, 1977). However, Pacific halibut movements and population structure are not fully understood and mixing may be more restricted than assumed, as evidenced by a number of local depletions in recent years (Hare[1]). A method for estimating movements over large distances is needed to improve the ability to identify populations and manage the harvest. Population structure and movement information is needed for management of several other high-latitude fisheries including Atlantic halibut (*Hippoglossus hippoglossus*), Pacific cod (*Gadus macrocephalus*) and Greenland turbot (*Reinhardtius hippoglossoides*) (Godø and Haug, 1988; Shimada and Kimura, 1994; Albert, 2002).

New methods using information collected by electronic tags, which contain miniaturized onboard computers, are providing location estimates of demersal marine fishes (see review in Arnold and Dewar, 2001). One such method, the tidal location method, has been used to geolocate North Sea plaice (*Pleuronectes platessa*) (Hunter et al., 2003). This method compares the tidal range and time of high

[1] Hare, S. R. 2005. Investigation of the role of fishing in the Area 4C CPUE decline. Int. Pac. Halibut Comm. Report of Assessment and Research Activities 2004:185–198. Int. Pac. Halibut. Comm, PO Box 95009, Seattle, WA 98145-2009.

water, as measured by the depth sensor of the electronic tag, to those predicted by tide models. Unfortunately, we are unable to use this method near Alaska because the water depth is much greater than in the North Sea. Deep water necessitates that the depth sensor of a tag have a greater range, which decreases depth resolution. Thus, tags used off Alaska have a depth resolution that is greater than the tidal range; therefore the tag cannot distinguish tidal fluctuations.

Another tagging method has been used to geolocate Baltic Sea cod (*Gadus morhua*) (Neuenfeldt et al.[2]). This method is based on combined data of depth, temperature, and salinity obtained by electronic tags attached to cod. Hydrographic fields obtained from hydrodynamic modeling are used as a geolocation database to identify daily locations of fish by comparison with the environmental data collected by each electronic tag. Unfortunately, the tags that we used are not available with a salinity sensor and hydrodynamic models of the area are not accurate on the bottom (Hedstrom[3]).

Ambient light data collected by electronic tags may be used to calculate daily estimates of latitude and longitude of fish. Geolocation by light has been implemented successfully on a variety of pelagic species to discern their daily position and movement patterns (Gunn and Block, 2001; Schaefer and Fuller, 2002; Itoh et al., 2003; Sibert et al., 2003).

However, no studies have been conducted to evaluate light-based geolocation estimates from tags attached to demersal fish, nor from fish inhabiting high latitudes. Unfortunately, light levels in deep and high-latitude waters may be low and if the water is turbid, the light may be attenuated very quickly, thus hindering position estimates. Additionally, many demersal fishes inhabit a depth range where geolocation by light has not been evaluated at any latitude.

The goal of this study was to examine the feasibility of using ambient light geolocation for estimating demersal fish movements in high latitudes. This was accomplished by the following procedures: 1) by comparing daily latitude and longitude estimates from two proprietary software types developed by Wildlife Computers, 2) by examining latitude and longitude estimates as a function of depth, and 3) by examining *in situ* latitude and longitude estimates of pop-up archival transmitting (PAT) tags attached to wild Pacific halibut.

Materials and methods

The pop-up archival transmitting tag (PAT, Wildlife Computers, Redmond, WA, vers. 2.0) is a miniature computer that is attached externally to a fish. The tag contains a clock and sensors that collect depth, temperature, and ambient light intensity data at user-specified intervals (Sibert, 2001). On a programmed date, the PAT tag disengages from the fish, floats to the surface, and transmits summaries of the recorded temperature, depth, and light data to Argos satellites; the data are then retrieved by the investigator. If the tag is retrieved, the complete archival record of temperature, depth, and ambient light data may be obtained.

From October 2000 to March 2002, a pilot study was conducted to assess the feasibility of using PAT tags as a tool for identifying critical habitat of demersal fishes in high latitudes (Seitz et al., 2002, 2003). Geoposition estimates were made from light data collected in three experiments in which PAT tags were attached to 1) Pacific halibut in outside aquaria, 2) a stationary mooring, and 3) wild Pacific halibut *in situ*. The temperature and depth data from the wild Pacific halibut experiment and their Argos-based final locations have been reported previously (Seitz et al., 2003).

In the first experiment, two Pacific halibut were captured, transported live to outside aquaria at the Alaska SeaLife Center (Seward, Alaska; 60.099°N, 149.440°W) and tagged on 18 Oct. 2000 with PAT tags programmed to record light intensity every minute. The tags were retrieved on 1 May 2001, and the longitudes and latitudes of Pacific halibut estimated from the tag data were compared with the known location of the Pacific halibut in the aquaria.

A second experiment was conducted by using a fixed mooring to examine latitude and longitude estimates as a function of depth. From December 2000 to April 2002, four PAT tags were attached to a stationary mooring line (the NOAA Alaska Observing System's "GAK-1" mooring) in Resurrection Bay, Alaska (59.852°N, 149.330°W) at depths of 27, 57, 96 and 146 m. These tags were attached to four different current vanes on the mooring line so that their light sensors faced up.

In a third experiment, to evaluate the performance of the light sensor and geolocation algorithm *in situ*, fourteen wild Pacific halibut (108–165 cm fork length) were captured, tagged, and released in November 2000, March 2001, and July 2001 from a commercial longlining vessel in Resurrection Bay, AK, and off Cape Aialik, AK (for details, see Seitz et al., 2002, 2003). Light data were recovered from eight tags. PAT tags were tethered externally to each study animal by a piece of monofilament fishing line secured to a titanium dart that was inserted into the dorsal musculature of the fish. At a user-specified date and time, the PAT tag corroded the pin to which the tether was attached, thus releasing the tag from the animal. The tag floated to the surface and transmitted summarized data records through the Argos satellite system.[4] After the tag popped-up to the

[2] Neuenfeldt, S., H.-H. Hinrichsen, and A. Nielsen. 2004. A method to geolocate eastern Baltic cod by using Data Storage Tags (DSTs), 14 p. Int. Coun. Explor. Sea CM/L:06. Int. Coun. Explor. Sea, H.C. Andersens Boulevard 44-46, DK-1553, Copenhagen V, Denmark.

[3] Hedstrom, K. 2005. Personal commun. Artic Region Supercomputing Center, Univ. Alaska Fairbanks, PO Box 756020, Fairbanks, AK 99775.

[4] Service Argos, Inc. (http://www.argosinc.com). [Accessed on: 13 December 2005.]

surface, its location was determined by the Doppler shift in the transmitted radio frequency in successive uplinks (Keating, 1995). The endpoint position was the first location class (LC) estimate reported in the LC1-3 range, which all have error estimates <1.0 km.

The basis of light-based geolocation is the estimation of times of sunrise and sunset. Two proprietary programs developed by the Wildlife Computers, Argos Message Processor (AMP, vers. 1.01.0007) and Time Series Processor (TSP, vers. 1.01.0008), were used to extract times of sunrise and sunset from light intensity data. AMP identified daily sunrise and sunset times from light data transmitted through Argos satellites or directly from complete archival light records. TSP could be used only to identify sunrise and sunset times from complete archival light data from PAT tags that were physically recovered.

In the next phase, another Wildlife Computers program, Global Position Estimator (GPE, vers. 1.01.0005), used the sunrise and sunset times to calculate the daily longitude and latitude of tags. First, we rejected days with light level curves that did not exhibit smoothly sloping light levels from high to low or low to high (Fig. 1). GPE was used to calculate longitude for the remaining data based on the local noon time of the tag (mean of the sunrise and sunset times). Estimated longitude values that were not possible for a fish released in the Gulf of Alaska were rejected from the data set. For example, an impossible longitude was one that placed the tag on land or outside the published range of the Pacific halibut (i.e., to the west of Hokkaido, Japan (140°E) or to the east of Santa Barbara, CA (117°W; Mecklenberg et al., 2002)). Once longitude was estimated, latitude was estimated by GPE, which used the "dawn and dusk symmetry method" (Hill and Braun, 2001; Musyl et al., 2001). Daily latitude estimates were the theoretical location of expected light levels that best matched the observed light levels measured by the tag. Latitude outliers were removed in the same manner as that used for longitude outliers. For all three experiments, the number of days with geolocation estimates was defined as the days that produced latitude and longitude estimates, after "bad" light curves (Fig. 1) and outliers were removed.

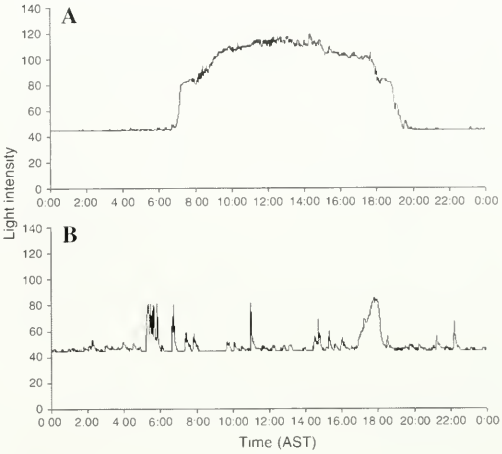

Figure 1

Examples of "good" and "bad" light curves. "Good" light curves (**A**) have smoothly sloping sunrise and sunset events. "Bad" light curves (**B**) do not have smoothly sloping sunrise and sunset events and produce outlying longitude and latitude estimates. The "good" light curve is from 2 March 2001 and the "bad" light curve is from the same tag on 10 March 2001. AST = Alaska standard time.

For the tags with known positions in the tank and mooring experiments, we calculated bias and error magnitude based on true locations. Daily positional bias was calculated as the true position minus the estimated position (signed distance between positions), and daily error magnitude was the absolute value of the bias (distance between points). For the tank experiment, we pooled the data from the two tags. Mean error magnitudes of software types were compared by using a two-tailed *t*-test. For the fixed mooring experiment, we calculated mean positional bias and mean error magnitudes for each tag and software combination. Mean biases were compared to a hypothetical bias of zero by using a two-way (tag and software) ANOVA model (vers. 8, proc GLM, SAS, Cary, NC). Mean error magnitudes were compared by using an ANOVA with a Tukey-Kramer test (Kramer, 1956; vers. 8 proc GLM). For both bias and error magnitude, the means are a measure of accuracy and the standard deviations are a measure of precision.

For wild fish, it was impossible to know the true daily position of each fish for the duration of the experiment. However, for three of the eight tags released on wild fish, geolocation estimates were produced in the first or last six days of deployment. Therefore, we compared the estimated positions of the tags for the six days immediately following release of the tags and for the six days before recapture of the tags or before tags transmitted data to Argos satellites. All three of these tags were physically recovered and TSP produced estimates for all tags. AMP produced plausible estimates for one tag only because other estimates were rejected as outliers. For each comparison, we calculated the mean bias and mean error magnitude, assuming that the fish was stationary (or nearly so) during the first and last six days of the deployment.

Results

All 14 tags, with the exception of one, functioned properly for the duration of the three experiments. The one exception, attached to a halibut *in situ*, was deployed for 234 days, but it provided data for only the first 42 days because the battery failed. Tracking durations for AMP (range: 42–479 days) were always equal to or greater than the tracking durations for TSP (range: 42–348 days) because the memory for the archival data filled up before the summary data memory.

In the tank experiment, TSP was a better estimator of longitude than AMP. TSP rejected fewer outliers and produced a higher percentage of days with longitude estimates (89.5%) than AMP (82.9%). Additionally, the mean longitude error magnitude for TSP (1.0° ±1.1° SD) was significantly smaller than that of AMP (2.0° ±3.2° SD) (t=5.63, df=650, P<0.0001). Longitude errors were larger from late-fall to mid-winter in both tags when estimated by AMP, but not TSP. The mean longitude bias of TSP (−0.12° ±1.5° SD) was significantly smaller than that of AMP (−0.64° ±3.7° SD) (t=2.3, df=650, P=0.0215). TSP was not significantly biased and AMP had a significant mean longitude bias.

In the tank experiment, TSP also produced a higher percentage of days with latitude estimates (88.2%) than AMP (81.6%). However, there was not a significant difference in the mean latitude error magnitude between TSP (4.2° ±5.1° SD) and AMP (4.4° ±4.2° SD) (t=0.36, df=641, P=0.7155). The mean positional bias of TSP (−0.02° ±6.7° SD) was not significantly different (t<0.0001, df=641, P=0.9730) from that of AMP (−0.08° ±6.1° SD) and neither software type had a significant mean positional bias.

In the fixed mooring experiment, TSP was a better estimator than AMP of longitude. In general, the tags produced fewer longitude estimates as depth increased, and at each depth, TSP generated more estimates than AMP (Fig. 2). The mean longitude error magnitude for both programs increased at greater depth (Fig. 3). The mean error magnitude of AMP and TSP estimates was not significantly different at 27 m and 57 m (P>0.50), but AMP estimates quickly degraded starting at 96 m (Fig. 3). For the tags at 96 m and 146 m, the mean error magnitudes for TSP estimates were significantly smaller (P<0.0001) than the AMP estimates of the same tags. The mean longitude biases of both AMP and TSP were generally to the west (positive values) of the actual position of the tags, except for AMP at 96 m (Fig. 3). In several cases, the mean biases were relatively small for both AMP and TSP, however both had large variances.

As with the longitude estimates in the fixed mooring experiment, the percentage of days with latitude estimates decreased at greater depths (Fig. 2). Unlike longitude, latitude was not estimated accurately by the tags. Mean latitude error magnitude was significantly smaller for TSP than for AMP at all depths, except 146 m (Fig. 3). The mean error magnitude for both AMP and TSP showed no relationship to increasing depth (Fig. 3). The mean latitude biases of the tags in the fixed mooring experiment were greater than the mean longitude biases, and the biases by AMP were more variable than those of TSP (Fig. 3). Like longitude in the fixed mooring experiment, latitude was not estimated at 146 m during the winter and spring. The time span without geolocation estimates was longer for latitude (242 days) than for longitude (165 days).

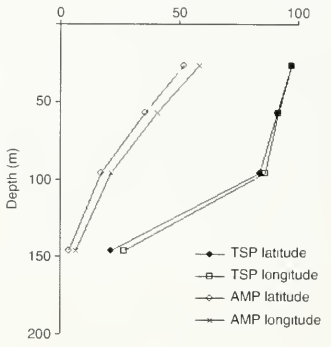

Figure 2

Percentage of days with longitude and latitude estimates as a function of depth in the fixed mooring experiment. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to calculate daily longitude and latitude.

In the wild fish experiment, four tags reported only to Argos satellites and geoposition was estimated from summary data by using AMP. The percentage of days with longitude estimates ranged from 0.0% to 2.3% (mean=1.1% ±1.0% SD), whereas the percentage of days with latitude estimates ranged from 0.0% to 1.5% (mean=0.6% ±0.7% SD). The other four tags were physically recovered and geoposition was estimated by using both summary data for AMP and detailed data for TSP. For AMP, the percentage of days with longitude estimates ranged from 0.0% to 12.0% (mean=5.8% ±5.9% SD), whereas the percentage of days with latitude estimates ranged from 0.0 to 7.9% (mean=3.4% ±3.5% SD). For TSP, the percentage of days with longitude estimates was higher, ranging from 9.9% to 32.3% (mean=19.7% ±9.4% SD) and days with latitude estimates ranged from 9.9% to 26.6% (mean=16.9% ±7.2% SD).

The mean error magnitude of the longitude estimates for AMP (n=4; 2.98° ±2.43° SD) was slightly larger than that of TSP (n=10; 2.23° ±2.38 SD°). However, the mean error magnitude of the latitude estimates for AMP (n=4; 2.76° ±1.59° SD) was approximately half that of TSP (5.65° ±4.11° SD). The mean longitude bias

for AMP (2.95° ±2.47° SD) was larger and to the east of that of TSP (−1.32° ±3.04° SD). The mean latitude bias was relatively small for both AMP (0.56° ±3.50° SD) and TSP (0.10° ±7.26° SD); however both had large variances and thus the estimates were not precise. In several cases, the longitude estimates were within one degree of the true position and there did not appear to be a pattern of over- or underestimating longitude.

Discussion

Geolocation estimates determined from ambient light data in high latitudes is equally effective as in lower latitudes. Similar to results from previous geolocation evaluations (Welch and Eveson, 1999, 2001; Musyl et al., 2001; Teo et al., 2004), our longitude estimates were in general more accurate and precise than latitude estimates. Therefore, longitude estimation by light is a promising technique for discerning large-scale movement of demersal fishes in coastal Alaska, but latitude estimation determined from light data only will not be adequate for these purposes.

This study was unique in testing light-based geolocation in depths greater than 60 m. The results demonstrate the importance of evaluating geolocation by light for the entire depth range of the species of interest. Testing only in the near-surface waters would be misleading because the percentage of days with estimates from tags at shallower depths was much greater than the percentage of days with estimates from tags at greater depths—the depths which halibut most frequently inhabit (Seitz et al., 2003).

The accuracies of the longitude estimates in this study were comparable to those at lower latitudes and similar water depth. Errors are discussed in linear distance (Table 1) to account for the fact that a degree of longitude varies with latitude and to facilitate comparisons to previous studies. The longitude errors from the tank experiment were generally similar to the errors produced in a comparable experiment where tags were placed on a stationary mooring at a depth of 10 m (Welch and Eveson, 1999). The tags submerged at deeper depths in the fixed mooring experiment also showed a longitude error magnitude similar to that of location estimates from tags in the offshore region of the Gulf of Alaska at 50°N, 145°W (Musyl et al., 2001; Welch and Eveson, 2001). The longitude biases were only slightly larger than those from tags on a stationary mooring near Hawaii (Musyl et al., 2001).

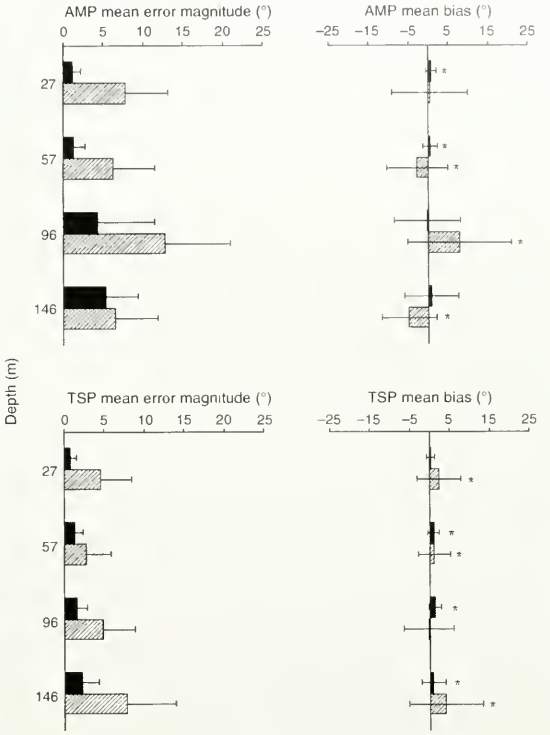

Figure 3

Mean (±SD) positional errors and bias in the fixed mooring experiment. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to calculate daily longitude (black bars) and latitude (hatched bars). Asterisks (*) indicate mean positional biases that were significantly different from zero in tests with two-way ANOVA. A negative bias indicates that a position estimate was either north or east of the known position, and a positive bias indicates that a position estimate was either south or west of the known position.

The minimum movement of a fish that was discerned by light-based geolocation in our experiment is the absolute sum of the error magnitude and bias. The sum of the error magnitudes and biases of TSP were generally smaller than those of AMP; therefore TSP was a better estimator of light-based geoposition than AMP and can be used to discern movement at a finer scale. The tank and fixed mooring experiments indicated that longitude estimation by TSP is able to discern movements of approximately ±200 km for depths as great as 150 m and AMP is able to discern east-west movements of approximately ±350 km at 150 m deep. Geolocation by light will be able to discern the large-scale movements

Table 1

Linear distance of mean error magnitude for the tank, fixed mooring, and wild fish experiments. Longitude and latitude were calculated from light intensity data collected by pop-up archival transmitting tags in two programs, Argos Message Processor (AMP) and Time Series Processor (TSP). Mean error magnitude was calculated by averaging the absolute value of the difference of the true position and the estimated position of the tag for each day of the experiment. Total error was the vector distance from the known location of the tag when longitude and latitude errors were combined. The great circle formula was used to convert angular errors to linear distances.

			AMP			TSP		
Experiment	Tag	Depth (m)	Longitude (km)	Latitude (km)	Total error (km)	Longitude (km)	Latitude (km)	Total error (km)
Tank	00-0740	0	139.1	500.9	519.8	62.9	500.9	504.8
Tank	00-0741	0	83.5	480.8	488.0	48.4	445.2	447.8
Mooring	00-0822	27	66.2	873.7	876.2	41.7	505.3	507.0
Mooring	00-0826	57	74.6	696.8	700.7	74.6	310.5	319.4
Mooring	00-0806	96	241.5	1421.3	1441.7	89.6	540.9	548.3
Mooring	00-0824	146	299.3	726.8	786.0	123.5	871.5	880.2
Wild fish	All tags	90–202	165.8	307.2	362.6	124.1	628.9	392.0

of Pacific halibut because this species performs spawning migrations of over 1100 km (Loher[5]). Additionally, with recovery rates as high as 50% in area-specific conventional tagging experiments (Kaimmer, 2000), TSP can could be used for a large portion of tag recoveries in future experiments.

At the largest scale, we were able to discern with confidence whether the wild Pacific halibut in this study were in the Gulf of Alaska or Bering Sea. Individual estimates were subject to occasional large errors and therefore caution should be practiced when using these estimates to represent the true position of fish. Examining patterns in estimates is more useful for determining locations. To reach the Bering Sea (west of 157°W), a Pacific halibut would have to migrate from the Gulf of Alaska through False Pass (163.5°W), which is the eastern-most connection between the two areas. The wild Pacific halibut in our study appeared to remain within the Gulf of Alaska, because fewer than 5% of the longitude estimates were to the west of 163.5°W, and those appeared to be erroneous because adjacent estimates did not consistently corroborate them. Trends in longitude estimates did not provide sufficient evidence to indicate that any of the wild Pacific halibut swam to the Bering Sea.

A variety of uncontrollable factors can cause intrinsic and extrinsic errors in geolocation estimates. The predominant source of intrinsic error is refraction in the earth's atmosphere that is caused when light travels through the atmosphere and is bent by air and other molecules (Schaefer and Liller, 1990). This error limits the absolute accuracy of the estimates to a constant 0.32° longitude and a minimum of 0.7° latitude (Hill and Braun, 2001). Extrinsically, light levels may be drastically influenced by changing external conditions, such as waves, water turbidity, diving behavior of the animal, biofouling, and cloud cover (Metcalfe, 2001). In particular, the Alaska coastal region frequently experiences large changes in weather systems that change cloud cover and sea-state on a daily, or even hourly, basis. One final consideration for errors is that accurate location estimates rely on unobstructed horizons. If the horizon is obstructed, such as by the mountains surrounding the coast of Alaska, it alters the time(s) of apparent sunrise (and sunset), thus affecting geolocation estimates. The tank experiment was conducted in a deep, north-south fjord whose walls obstructed the horizon, and the fixed mooring experiment was adjacent to an island on the east and to steep coastal mountains to the west. Undoubtedly, these false horizons accounted for part of the errors and bias.

One shortcoming discovered in the fixed mooring experiment was a conspicuous gap in longitude and latitude estimates from December to June at 146 m. This six-month gap was probably the result of low ambient light levels during the winter associated with high latitudes. It is unknown why the gap lasted into the summer when ambient light drastically increased. However, for practical application in studies of Pacific halibut migration, light-based geolocation estimates will capture some individual migrations to the spawning grounds as some Pacific halibut begin migrating in October and arrive on the continental slope by early November (Seitz et al., 2003).

We may be able to increase the number of location estimates with some fine-tuning of both software types. Several days were rejected because of poor light readings. However, some days had smoothly sloping sunrise and sunset events that appeared to be sufficient for accurate geolocation estimates, but the software mis-

[5] Loher, T. 2005. Personal commun. Int. Pac. Halibut. Comm, PO Box 95009, Seattle, WA 98145-2009.

identified sunrise and sunset. This misidentification typically occurred because there were occasional aberrant light readings. The geolocation software identified these as sunrise, sunset, or both, and therefore gave bogus position estimates. There is an option to override these aberrant sunrise and sunset times when using TSP because the software allows manual selection of sunrise and sunset. For our study, we opted not to do this because we did not want to introduce subjectivity into sunrise and sunset times. We suggest that the software be modified by the manufacturer to select the next best times for sunrise and sunset so that the investigator may reject aberrant light readings and yet allow the software to objectively choose sunrise and sunset.

In future studies, we hope to improve geoposition estimates by statistically filtering (Sibert et al., 2003) or smoothing longitude estimates and by incorporating additional sensor data. For example, in conjunction with light data, tag-measured sea-surface temperature (SST) can be compared to remotely sensed SST, to significantly improve geolocation estimates (Teo et al., 2004). In the case of demersal fish that rarely, if ever, visit the sea surface, maximum daily depth can be used as representative of the total water depth in the region. We can compare the maximum daily depth sampled by an electronic tag to existing bathymetry data to estimate possible daily positions of the fish. We can then combine the geolocation estimated by light-level information with the depth information to yield a most plausible track of daily positions.

Accurate description of the movement of fish is the cornerstone of sound management plans for ensuring sustainable fisheries in the future (Hunter et al., 2003). Longitude estimation determined from ambient light data may be used to examine large-scale movements of demersal fish in high latitudes. There are several types of electronic tags—some designed for fish as small as 15 cm (Arnold and Dewar, 2001). Using this technique, we can describe large-scale spatial dynamics and migration of several commercially important demersal fish species.

Acknowledgments

This project was made possible through the expertise of Capt. Harold Kalve of the FV *Rocinante* during fishing operations; Dave Douglas, Dan Mulcahy DVM, and Julie Meka of USGS-Alaska Science Center; Susan Ingles, Richard Hocking, Pam Parker, Brian Mullaly, Jessica Dunning, and the staff at Alaska Sea Life Center; and Tom Weingartner, David Leech and the crew on the RV *Alpha Helix* from the University of Alaska Fairbanks. A special thanks to Devin Johnson for statistical assistance. Partial funding for this project was provided by the Exxon Valdez Oil Spill (EVOS) Trustee Council (Restoration Project 478) and the U.S. Geological Survey-Alaska Science Center. The Gulf of Alaska (GAK) 1 mooring is funded by the EVOS Trustee Council under a separate grant (Restoration Project 340). The findings presented by the authors are their own and not necessarily the position of the EVOS Trustee Council.

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Abundance and distribution of whale sharks (*Rhincodon typus*) in the northern Gulf of Mexico

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Abstract—Information on the seasonal abundance and distribution of whale sharks (*Rhincodon typus*) is largely unknown throughout range of the species. Between 1989 and 1998, three spatially and temporally intensive aerial surveys were conducted by the National Marine Fisheries Service, Mississippi Laboratories that provided information on seasonality, distribution, and aggregations of whale sharks in the northern Gulf of Mexico. Transects totaling 89,369 km were surveyed over the course of the study and a total of 119 whale sharks were counted during 81 sighting events. There was no statistical difference in the sightings per unit of effort (SPUE) of whale sharks between the eastern and western continental slope waters of the Gulf of Mexico. In the continental slope waters of the eastern Gulf of Mexico, whale sharks were more abundant during the summer than in the winter. In the western Gulf of Mexico, whale shark SPUE was significantly greater in the summer than during the fall or winter; there was no significant difference between summer and spring. There was also no significant difference in whale shark SPUE among spring, fall, and winter in the western Gulf of Mexico. Aggregations of whale sharks were seen only during the winter and summer, and there were significantly more individuals per aggregation during the summer. The largest aggregation of whale sharks observed during the study consisted of 23 individuals.

Manuscript submitted 8 January 2005 to the Scientific Editor's Office.

Manuscript approved for publication 13 January 2006 by the Scientific Editor.

Fish. Bull. 104:579–584 (2006).

Whale sharks (*Rhincodon typus*) are distributed in all tropical and subtropical marine waters of the world, with the exception of the Mediterranean Sea (Compagno, 1984). This species is considered vulnerable to extinction according to the World Conservation Union (IUCN)[1] partly because of a lack of information pertaining to its life history. Although the seasonality of whale sharks has been examined in two geographically discrete areas (Taylor, 1996; Duffy, 2002), no information exists for the seasonal distribution or relative seasonal abundance of this species over a broad spatial scale. The paucity of such information is probably attributable to logistical difficulties associated with collecting required data or to the expense of surveying large areas.

Whale sharks aggregate in areas of high biological productivity, and seasonal abundance of whale sharks could result from increased localized prey abundance. Whale sharks feed on a variety of organisms including invertebrates and teleosts (Compagno, 1984). Unlike basking (*Cetorhinus maximus*) and megamouth (*Megachasma pelagios*) sharks, which passively filter prey from the water column, whale sharks are capable of suction filter feeding (Colman, 1997). Although this feeding strategy enables whale sharks to capture a wider range of prey in terms of size, mobility, and diversity than other filter feeding elasmobranchs, this feeding strategy requires dense aggregations of prey in order for whale sharks to meet their energetic demands (Compagno, 1984). Feeding aggregations of whale sharks have been reported in the Atlantic, Indian, and Pacific Oceans and specifically in the waters off Belize, Western Australia, the Galapagos Islands, Mexico, New Zealand, and Thailand (Taylor, 1996; Clark and Nelson, 1997; Colman, 1997; Eckert and Stewart, 2001; Heyman et al., 2001; Wilson et al., 2001; Duffy, 2002).

The whale shark was first described in 1828 from a type specimen collected off the coast of South Africa (Penrith, 1972). The first record of a whale shark in the western North Atlantic Ocean was not reported until 1902 and it was 1937 before this species was documented in the Gulf of Mexico (Gudger, 1939; Baughman and Springer, 1950; Breuer, 1954). Since 1937 several authors have reported sightings of whale sharks in the Gulf of Mexico (Gudger, 1939, 1941; Baughman, 1947, 1950, 1955; Gunter and Knapp, 1951; Breuer, 1954; Springer, 1957; Clark and von Schmidt, 1965; Hoffman et al., 1981; Hoffmayer et al., 2005). However, these reports are restricted to spatially discrete areas, and most are primarily anecdotal and largely based on isolated observations of few individuals. In the present study we report the seasonality, rela-

[1] The World Conservation Union. 2005. http://www.redlist.org [accessed 5 January, 2006].

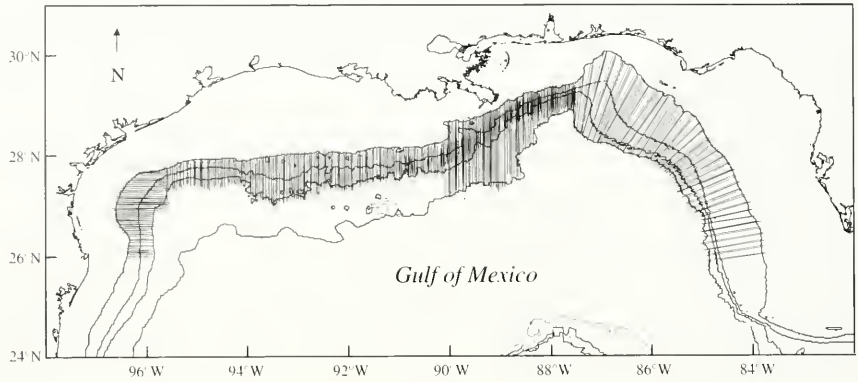

Figure 1

Transect lines surveyed by aircraft during three aerial studies conducted in the northern Gulf of Mexico from 1989 to 1998. Note that some lines overlap others, particularly in the eastern Gulf of Mexico. Bathymetric contours represent the 100-, 500-, 1000- and 2000-meter contours.

tive seasonal abundance, distribution, and aggregations of whale sharks observed in the northern Gulf of Mexico during three spatially and temporally intensive aerial surveys conducted by the National Marine Fisheries Service, Mississippi Laboratories.

Materials and methods

Between 1989 and 1998, three aerial surveys were conducted in the northern Gulf of Mexico with a DeHavilland Twin Otter turbine engine aircraft. The primary objective of one of these surveys, referred to as the Upper Continental Slope (UCS) Survey, was to examine species composition, distribution, and seasonality of cetaceans in the north-central Gulf of Mexico (Mullin et al., 1994). The purpose of the other two surveys, referred to as the Gulf of Mexico Cetacean Studies I (GulfCet I) and Gulf of Mexico Cetacean Studies II (GulfCet II) (Mullin and Hoggard[2]) surveys, was to assess possible impacts of petroleum industry activities on cetaceans and sea turtles in the Gulf of Mexico. Standard line-transect sampling methods were used for each survey (Buckland et al., 1993). Surveys were flown at a constant altitude and air speed of 229 m and 200 km/h, respectively. The aircraft was modified with a Plexiglas observation bubble on the port and starboard sides of the fuselage to permit an unobstructed view of the area along transect lines and a lateral view to each horizon. When fauna of interest were sighted, the pilot circled the area until all observed fauna were identified to the lowest possible taxa and the latitude and longitude of the sighting and numbers of conspecifics sighted were recorded. All survey effort was limited to waters associated with the continental slope in Beaufort sea states less than 4 and restricted to areas within the United States Exclusive Economic Zone (EEZ; Fig. 1). For all analyses and discussion, seasons were defined as spring (April–June), summer (July–September), fall (October–December), and winter (January–March).

The UCS survey was conducted from the summer of 1989 through the spring of 1990 and was carried out during all four seasons. The study area was located in the central northern Gulf of Mexico along the continental shelf break (~200-m isobath) south of the Mississippi River Delta and extended from the DeSoto Canyon (87°00′W) to the western edge of the Mississippi Trough (90°05′W). GulfCet I surveys occurred from 1992 to 1994 over continental slope waters in the western Gulf of Mexico between the United States and Mexico border (25°57′N) and the Mississippi–Alabama border (88°25′W) and were conducted during all four seasons (Mullin et al., 2004). GulfCet I transects began at the 100-m isobath and extended to the 1000-m isobath west of 90°00′W, and to the 2000-m isobath east of 90°00′W. GulfCet II surveys were conducted only during the winter and summer between 1996 and 1998 in the northeastern Gulf of Mexico and covered continental slope waters (100–2000 m deep) and a portion of the continental shelf (Mullin and Hoggard[2]). The entire spatial range of the three areas was surveyed within each season of operations. Because of the spatial overlap of the UCS and GulfCet II surveys, the central northern Gulf of Mexico and the western Gulf of Mexico were treated as a single region, referred to as "the western

[2] Mullin, K. D., and W. Hoggard. 2000. Visual surveys of cetaceans and sea turtles from aircraft and ships. *In* OCS Study MMS 96-0027, vol. II, Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations (R. W. Davis, W. E. Evans, and D. Würsig, eds.), p. 111–172. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA 70123.

Table 1

Summary of survey effort, number of whale shark (*Rhincodon typus*) sightings, and sightings per unit of effort (SPUE) by region, season, and survey. UCS=upper continental survey; GulfCetI=Gulf of Mexico Cetacean Studies I; GulfCet II=Gulf of Mexico Cetacean Studies II.

Survey and region covered	Season	Effort (km)	Number of sharks	SPUE
UCS—western Gulf of Mexico	winter	4382	1	0.23
	spring	7615	8	1.05
	summer	5321	14	2.63
	fall	3275	0	0.00
GulfCet I—western Gulf of Mexico	winter	12,645	13	1.03
	spring	12,645	20	1.58
	summer	12,942	43	3.32
	fall	11,756	7	0.60
GulfCet II—eastern Gulf of Mexico	winter	8348	3	0.36
	summer	10,440	10	0.96

Gulf of Mexico," in this article. Mobile Bay, Alabama (88°00′W) was considered to be the dividing line between the eastern and western Gulf of Mexico.

Sightings per unit of effort (SPUE) were calculated to correct for unequal effort among regions by dividing the number of sightings per season by the total survey effort during the same season and then multiplying the resulting value by 1000. Because aerial surveys were limited to summer and winter in the eastern Gulf of Mexico, data from these two seasons in this region were compared (by using a t-test) to data collected during surveys in the same two seasons in the western Gulf of Mexico to determine if mean whale shark SPUE was significantly different between the two areas. To determine if there was a season of peak whale shark SPUE in the western Gulf of Mexico a one-way analysis of variance (ANOVA) and the Student-Newman-Keuls test were employed. The Mann-Whitney test was used to determine if there was a significant relationship between season and number of individuals per aggregation. This test was selected because of the non-Gaussian distribution of these data. The location of each whale shark sighting was plotted on navigational charts, produced by the National Oceanic and Atmospheric Administration (Chart numbers 11006, 11300, 11340), to examine the associations of whale sharks with bathymetric features such as reefs and salt diapirs. Statistical tests were preformed according to the methods of Zar (1999) at a significance level of $P \leq 0.05$.

Results

Transects totaling 89,369 km were surveyed over the course of the study (Table 1). A total of 119 whale sharks were counted during 81 sighting events (Fig. 2). There was no statistical difference in the SPUE of whale sharks between the eastern and western continental slope waters of the Gulf of Mexico (t-test, df=4, t-value=1.06, P=0.35). Because survey effort in the eastern Gulf of Mexico was limited to summer and winter, it was not possible to quantitatively analyze whale shark seasonality in this region. However, results indicated that whale sharks are more abundant in the eastern Gulf of Mexico during the summer (SPUE=0.96) than in the winter (SPUE=0.36). There was a statistically significant difference in whale shark SPUE among seasons in the western Gulf of Mexico (ANOVA, df=7, F-ratio=12.97, P=0.02). The Student-Newman-Keuls test indicated that whale shark SPUE was significantly greater in the summer ($\bar{x}$= 2.98, SD=0.49) than during the fall ($\bar{x}$=0.30, SD=0.18) or winter ($\bar{x}$=0.63, SD=0.32). However, there was no significant difference between summer and spring ($\bar{x}$=1.32, SD = 0.38). There was no significant difference in whale shark SPUE among spring, fall, and winter.

Of the 119 whale sharks sighted over the course of the study, 45 were observed in aggregations—an aggregation being defined as the presence of two or more whale sharks in close proximity to one another. Seven aggregations, ranging in size from 2 to 23 individuals, were observed. Aggregations of whale sharks were seen only during the winter and summer and there were significantly more individuals per aggregation during the summer (Mann-Whitney test, W=12.0, P=0.05). Sixty-two percent (n=74) of whale sharks were not observed in association with conspecifics.

The majority of whale sharks observed were not associated with discrete areas of high bathymetric relief. Thirty-four of the whale sharks sighted were in close proximity to relatively small, high relief diapiric features dominated by coralline algae (Rezak et al., 1990); Ewing Bank (28°06′N, 91°02′W), Bright Bank (27°53′N, 93°18′W) and 28 Fathom Bank (27°55′N, 93°26′W). Of the seven aggregations observed during the surveys, three were associated with the aforementioned banks including the aggregation consisting of 23 individuals. The area of highest whale shark abundance was located in an area of approximately 16,800 km^2 and

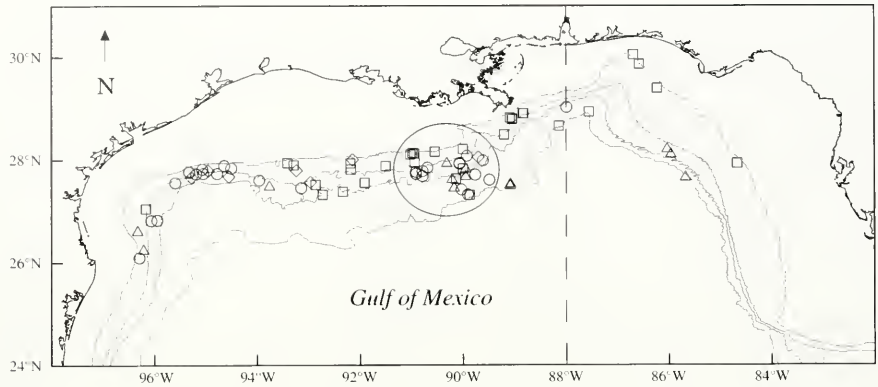

Figure 2

Locations (n=81) of whale sharks (*Rhincodon typus*) observed during aerial surveys in the northern Gulf of Mexico from 1989 to 1998. Dashed line demarks the separation between the eastern and western Gulf of Mexico as defined in our study. Area contained within the circle indicates region of highest observed whale shark abundance. Bathymetric contours represent the 100-, 500-, 1000- and 2000-meter contours. Location and season of sighting symbols: △ = winter, ○ = spring, □ = summer, ◇ = fall.

the center of their distribution was approximately 140 km southwest of the Mississippi River Southwest Pass (Fig. 2). Twenty-seven whale sharks were observed in this region over a four-year period.

Discussion

We observed whale sharks throughout the year in the Gulf of Mexico, and our study is the first to identify a broad region where whale sharks are present during all seasons and where they are perhaps resident throughout the year. The highest SPUE values that we observed occurred during the summer. Therefore, given the reported seasonality of whale sharks in the western Caribbean Sea (Heyman et al., 2001) and southeastern Gulf of Mexico (Gudger, 1941), it is reasonable to assume that a portion of the population migrates into the northern Gulf of Mexico during the spring and in winter moves into lower latitude waters, such as the Bay of Campeche and waters off the coast of Cuba. The only entrances to the Gulf of Mexico are through the Yucatan Channel and the Straits of Florida; therefore research with telemetry and satellite tagging in these regions would help determine the timing and routes of whale shark migrations and the period of residency within the Gulf of Mexico.

Whale sharks are more abundant in the western than in the eastern Gulf of Mexico. However, because the aerial surveys were limited to two seasons in the eastern Gulf of Mexico, little can be inferred from our data, except confirmation of the presence of whale sharks in the eastern Gulf of Mexico during the winter and the addition of summer to the seasonality of occurrence in this region. Because the survey reported in our study focused solely on continental slope waters, it is possible that whale sharks in the eastern Gulf of Mexico use continental shelf waters to a greater extent and, thus, were outside of the sampled area. Despite extensive effort over the broad upper continental slope off the west coast of Florida, no whale sharks were observed south of 27°38′N. However, at higher latitudes, 13 individuals were sighted in continental slope waters at depths ranging from 70 to 180 m. Because the upper continental slope is broader in the eastern than in the western Gulf of Mexico, it is possible that whale shark distribution in the eastern Gulf of Mexico is more diffuse than would be expected, especially if this species is associated with steep bathymetric relief, which promotes upwelling of nutrient rich waters. During our study, two whale sharks were observed at the head of the DeSoto Canyon, an upwelling area south of the Florida panhandle. A large aggregation (30–100 individuals) was found in this same area by Hoffmayer et al. (2005).

In the western Gulf of Mexico, whale sharks were observed in all sampled depth strata, and the spatial distribution of sightings was fairly continuous along the continental slope from Mobile Bay (88°00′W) to the United States/Mexico border (96°30′W; Fig. 2). Seasonally, whale sharks were present year round in the western Gulf of Mexico, except between 94°00′W and 95°35′W where they were observed only during spring and fall. Bimodality in seasonal occurrence in this region could be attributed to seasonal fluctuations in biological productivity and, thus, to prey availability resulting from ephemeral mesoscale phenomena such as Loop Current eddy formation, current reversals, and coastal jetting. For example, in the western Gulf of Mexico the Texas Current is capable of

generating localized upwelling on the continental shelf break, thus increasing primary productivity and the availability of prey species (Sahl et al., 1993). However, the Texas Current occasionally flows in a direction opposite to its normal eastward course because of wind forcing (Sahl et al., 1997). Such a reversal of direction in the Texas Current could affect productivity in this area and thus influence the seasonal abundance of whale sharks in this region. Given the stochastic nature of the physical oceanography of this region, additional research will be needed to determine if whale sharks make limited use of this area during discrete times of the year or if they are in fact present year round.

From observations made by commercial mariners in transit between the southern tip of Florida and unidentified ports in Texas, Gudger (1941) reported sightings of 68 whale sharks from a circular area in the north-central Gulf of Mexico with a diameter of approximately 280 km; however no specific locations were given. He concluded that the density of whale sharks in this area must be related to high prey densities. The area of highest regional abundance during the present study occurred in a circular area, bounded by 89°30′W and 91°00′W longitude, and having a diameter of approximately 165 km (Fig. 2). Three aggregations of between 30 and 100 whale sharks in this same area were reported by Hoffmayer et al. (2005). The safety fairway used by shipping traffic transiting between the eastern and western Gulf of Mexico crosses this area. It is probable, therefore, that the observations of whale sharks by commercial mariners reported by Gudger (1941) were in the same area. Because of nutrient loading from the Mississippi and Atchafalaya rivers, primary productivity is higher in this region of the Gulf of Mexico than in any other region (Lohrenz et al., 1999) and may explain the high localized abundance of whale sharks in this region. Other highly productive areas where whale sharks are known be present in relatively large numbers include Ningaloo Reef, Australia, and Gladden Spit, Belize (Taylor, 1996; Heyman et al., 2001).

The sighting of 23 whale sharks on 9 August 1993 was the largest aggregation observed during our study. The sharks, which were observed for about 35 minutes, were distributed over an area of approximately 2.6 km^2. Coral spawning occurred on 9 August 1993 at the East Flower Gardens (27°55′N, 93°36′W; Gittings[3]) which is approximately 33 km due west of the location of the aggregation sighting. A similar relationship between coral spawning events and increased localized abundance of whale sharks has also been noted to occur off the coast of Western Australia (Taylor, 1996). Future efforts should examine the relationship between annual coral spawning events and whale shark occurrence near the East Flower Gardens to determine if there is an annual migration of whale sharks to this area.

[3] Gittings, S. R. 1993. Personal commun. Science Program Manager, NOAA Office of National Marine Sanctuaries. 1305 East West Hwy, Silver Springs, MD 20910.

There are inherent difficulties associated with examining the seasonality of marine organisms using aerial surveys. This is particularly true when the species of interest is not obligated to surface waters where visual observations can be made. Because the whale shark is not a surface obligate species, factors such as changes in feeding behavior resulting from seasonal variability in the vertical distribution of prey species could have introduced significant bias into our sighting data, subsequent analyses, and data interpretation. We assumed that no differences exist among seasons in the amount of time whale sharks spend at or in close proximity to the surface. Using telemetry and archival tags, Gunn et al. (1999) determined that whale sharks spend 17–53% of their time at the surface during daylight hours off the coast of Australia. Over periods ranging from 28–1144 days, Eckert and Stewart (2001) tracked vertical movements of whale sharks through the water column in the Sea of Cortez using satellite tags. They concluded that during all seasons whale sharks spend greater than 80% of their time at depths of 10 m or less during all seasons—depth well within the photic zone of continental slope waters of the Gulf of Mexico. The findings of both Gunn et al. (1999) and Eckert and Stewart (2001) support our assumption.

Due to the economic value of their meat, fins, and liver oil, whale sharks have recently been designated as vulnerable to harvesting-induced extinction by the IUCN (Stewart and Wilson, 2005). Furthermore, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has placed the whale shark under Appendix II, which limits the trade of whale shark products among cooperating nations (Stewart and Wilson, 2005). Within the United States EEZ, the retention of whale sharks caught commercially or recreationally is prohibited (NMFS, 1993). However, because whale sharks are highly migratory and their movements cross numerous boundaries, detailed information on their abundance and seasonal distribution is needed to ensure their well being.

Acknowledgments

We thank W. Hoggard, S. O'Sullivan, and C. Roden for participating in the surveys and for their valuable suggestions. We also thank R. Avent, C. Gledhill, D. Hanisko, A. Jahncke, K. Mitchell, and K. Rademacher who assisted us in varying capacities. Comments by E. Clarke, M. Grace, T. Henwood, C. Hubard, C. Jones, K. Maze-Foley, S. Nichols, C. Roden, and the three anonymous reviewers significantly improved the manuscript. The research was authorized under Marine Mammal Research permits 738 and 779-1339 issued to the SEFSC, and was supported by interagency agreements between the NMFS-SEFSC and U.S. Geological Survey, Biological Resources Division (no. 1445-IA09-96-0009); and the NMFS-SEFSC and Minerals Management Service, Gulf of Mexico Region (nos. 15958 and 14-12-0001-30398).

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Effects of a simulated fishing moratorium on the stock assessment of red porgy (*Pagrus pagrus*)

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Abstract—Much of the information available on the population status of a harvested fish species is obtained from landings data. When fishing restrictions are in place, fishery-dependent data are reduced and assessments rely more heavily on fishery-independent data. Stock assessments of red porgy (*Pagrus pagrus*) have shown a declining population and have led to a number of management measures, including a moratorium on fishing this species. To investigate how a lack of fishery-dependent data during a moratorium would affect stock assessment results for red porgy, we conducted simulations representing a range of periods of moratorium. As data were removed from the model, stock status indicators and projections became increasingly variable. Projections estimated that a 12-year moratorium would be needed for stock rebuilding, but simulations showed that uncertainty surrounding stock assessment estimates would increase after three years without fishery-dependent data. Unless additional data are collected during periods of strict fishing regulations, it may be difficult to accurately assess the length of time needed for the stock to rebuild and to assess the population status.

Manuscript submitted 28 March 2005 to the Scientific Editor's Office.
Manuscript approved for publication 19 January 2006 by the Scientific Editor.
Fish. Bull. 104:585–592 (2006).

For commercial or recreational fisheries, a large portion of the information available for assessment of the population status of a species is obtained during harvesting operations. When harvest restrictions are in place, fishery-dependent data are reduced and assessments become more reliant on fishery-independent data. During a moratorium, harvest ceases completely and new methods may be required to assess the status of the stock. It is assumed that stock assessment results accurately portray the current population and that these results are used in policy decisions affecting future stock status. However, stock assessment results are not solely a product of the population being assessed, but are also a function of stock status, data sources, and sample size. Although most stock assessments include close evaluation of data sources, few assessments include the quantification of potential effects of changes in fishery-dependent data as a byproduct of changing harvest restrictions. We therefore investigated the effects of the reduced availability of fishery-dependent data on stock assessment results and management decisions.

To accomplish this goal, we conducted model simulations for red porgy (*Pagrus pagrus*) that is found off the coast of the southeastern United States from North Carolina to Florida. This reef-associated fish is an important resource for commercial and recreational fisheries (Huntsman et al., 1978; Low et al., 1985). Red porgy have an extensive native range and inhabit coastal waters on both sides of the Atlantic Ocean in both hemispheres (Pajeulo and Lorenzo, 1996; Labropoulou et al., 1999; Hood and Johnson, 2000). They are associated with live-bottom reef habitats on rocky outcroppings and therefore have a patchy distribution off the southeastern United States (Grimes et al., 1982). Red porgy are protogynous hermaphrodites; females dominate the smaller size classes, and males occur at all ages (Manooch, 1976). Females generally reach maturity from age-1 to age-2 at approximately 300 mm total length, and the majority of red porgy age-5 and older are mature males (Hood and Johnson, 2000).

Red porgy have been harvested extensively by three major fisheries (Fig. 1): commercial, recreational, and a fishery comprising large-scale charter boats called "headboats" (Huntsman et al., 1978). All three fisheries use mainly hook-and-line gear and target a wide variety of temperate reef fishes (Chester et al., 1984), not exclusively red porgy. In the early 1980s, the red porgy stock began showing signs of decline (Collins and Sedberry, 1991; Vaughan et al., 1992). As the stock decline became more evident, the minimum size limit was raised (Table 1) by the South Atlantic Fishery Management Council (SAFMC), the group mandated with managing red porgy and other fish off the coast of North

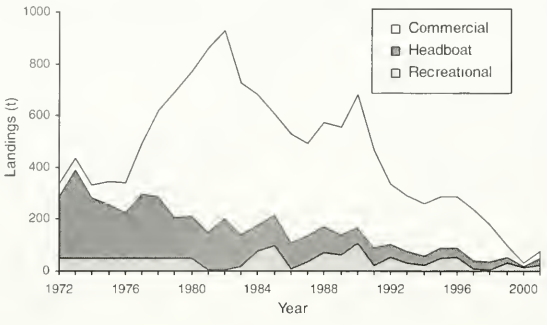

Figure 1

Landings (in metric tons) of red porgy (*Pagrus pagrus*) off the coast of the southeastern United States for the commercial, recreational, and headboat fishery sectors from 1972 through 2001.

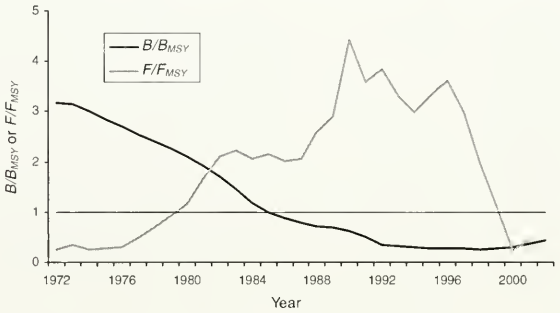

Figure 2

Relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}) for red porgy (*Pagrus pagrus*), as estimated in SAFMC (see Footnote 3 in the general text). The horizontal line represents $B=B_{MSY}$ and $F=F_{MSY}$.

Carolina, South Carolina, Georgia, and eastern Florida (SAFMC[1]). However, red porgy abundance continued to decrease (Vaughan and Prager, 2002), such that an emergency moratorium was put into place (Table 1) prohibiting the harvesting of red porgy by all fishery sectors. Following debate on the actual severity of the population decline and uncertainty surrounding the stock assessment, the moratorium was relaxed a year later to a seasonal closure, a recreational bag limit, and a commercial bycatch allowance (Table 1; SAFMC[2]). A recent stock assessment (Fig. 2; SAFMC[3]) identified this red porgy stock as having low biomass, but not as being currently overharvested. The strict harvest regulations applied to red porgy led to SAFMC concerns regarding the ability of scientists to accurately assess a population under a moratorium when fishery-dependent data are unavailable.

[1] SAFMC (South Atlantic Fishery Management Council). 1991. Final, amendment number 4, regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the fishery management plan for the snapper grouper fishery of the South Atlantic region, 99 p. + appendices. South Atlantic Fisheries Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

[2] SAFMC (South Atlantic Fishery Management Council). 2000. Final, amendment number 12 to the fishery management plan for the snapper grouper fishery of the South Atlantic region, 159 p. + appendices. South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

[3] SAFMC (South Atlantic Fishery Management Council). 2002. Southeast Data, Assessment, and Review (SEDAR) stock assessment for red porgy, 39 p. South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

Table 1

History of fishing regulations for red porgy (*Pagrus pagrus*) applied to both commercial and recreational fisheries, unless otherwise specified.

Regulation period	Regulation details	Regulation period	Regulation details
To 1992	No size, bag, or trip limits or closures	Sept 1999 to Aug. 2000 (moratorium)	No landings permitted
Jan 1989 to present	Trawl gear banned	Aug 2000 to present (Amendment 12)	356-mm minimum size limit; 1-fish recreational bag limit; Jan–Apr commercial closure; 22.7-kg commercial trip limit
1992 to Jan 1999	305-mm minimum size limit		
Feb 1999 to Aug 1999 (Amendment 9)	356-mm minimum size limit; 5-fish recreational bag limit; Mar–Apr commercial closure		

Red porgy is a relatively well-studied species; more than 30 years of information are available. However, the majority of the data for this species is a direct result of fishing operations. Fishery-dependent data for red porgy include landings (number of fish) from commercial, recreational, and headboat fisheries, as well as large sample sizes of lengths from these fisheries (Table 2; Huntsman et al., 1978; Low et al., 1985; NMFS[4]). The headboat fishery also provides an abundance index based on catch-per-unit-of-effort data. Although fishery-dependent data provide large sample sizes and a relatively long time series, there are a number of problems associated with this information source. Fishery-dependent statistics have been affected by frequent changes in regulations, economics, technology, and gear (Collins, 1990) that may cause difficulties for comparisons of landings, abundance indices, or lengths among years. Moreover, harvest data have inherent biases due to the nature of the fishery, which attempts to maximize catch, selects fishing areas nonrandomly, and targets larger size classes of fish.

In an attempt to compensate for some of the biases potentially present in harvest data, the National Marine Fisheries Service (NMFS) instituted the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program in 1979. During this annual survey, fishery-independent data are collected on a variety of reef fishes in waters from North Carolina to Florida (Collins, 1990; Harris and McGovern, 1997). In the MARMAP survey standardized gear types are used and known amounts of effort are applied to sample randomly selected sites between May and August (Collins, 1990), during which information on length, weight, age, sex, fecundity, and level of maturation are collected. An abundance index is also calculated for each gear type.

[4] NMFS (National Marine Fisheries Service). Fisheries Statistics Division. 2005. Website: http:www.st.nmfs.gov/st1 [accessed on 31 January 2005].

The MARMAP survey and other well-designed fishery-independent surveys are extremely useful for stock assessments because standardized gears are used with known efforts in documented locations, which constitute a statistically valid experimental design that facilitates comparisons among years, areas, and gear types (Collins and Sedberry, 1991). However, the MARMAP survey does not provide information on harvesting, and the survey's sampling methods are inherently different from fishery-dependent sources. Therefore, MARMAP data cannot serve as an absolute substitute for fishery-dependent information in existing stock assessment strategies. In addition, MARMAP sample sizes are much smaller than those from fishery-dependent sources, particularly for length-frequency data; 92% of samples for length-frequency estimates were obtained from fishery-dependent sources (Table 2).

In a highly restricted or closed fishery where fishery-dependent data are limited, information from fishery-independent sources may be the only data available to managers. This decreased amount of data could affect stock assessment results, including the estimation of stock status indicators and benchmarks used in management. It is therefore important to understand how to best use both fishery-independent and fishery-dependent data in assessments of red porgy and other species, both in unrestricted and heavily restricted fisheries.

During a moratorium or other period of strict regulation, the reduction in fishery-dependent data may increase variability surrounding status indicators and management benchmarks. We quantified the increase in variability for red porgy by using stock assessment model simulations and projections, and we identified how the uncertainty surrounding estimates could affect management decisions. By evaluating the effects of a lack of data before harvest restrictions are put in place, managers will be able to identify future data needs, improving their ability to assess and manage species of concern.

Table 2

Sample sizes for estimation of lengths and ages of red porgy (*Pagrus pagrus*) from fishery-independent (Marine Resources Monitoring, Assessment, and Prediction, [MARMAP] survey) and fishery-dependent (commercial and headboat fisheries) sources. The stock assessment model covered 1972–2001; therefore "model years" is equal to a span of 30 years.

Data source	Samples	Years	Samples per model year	Percentage
Lengths				
MARMAP	11,649	17	388	8.2
Commercial	81,625	26	2721	57.4
Headboat	49,012	30	1634	34.4
Total	142,286		4743	
Ages				
MARMAP	5274	13	176	57.5
Commercial	1250	4	42	13.7
Headboat	2645	4	88	28.8
Total	9169		306	

Materials and methods

Stock assessment model

The simulations to determine impacts of a lack of fishery-dependent data involved the use of a recent stock assessment model for red porgy, a forward-projecting age-structured model developed during the Southeast Data, Assessment, and Review (SEDAR) stock assessment workshop. The model was an expansion of the Methot (1989) stock-synthesis model and is similar in structure to models used in assessment of cobia (Williams, 2001). With the red porgy model, we simulated a population through time, applying annual fishing mortality, natural mortality, recruitment, and growth (SAFMC[3]) while attempting to statistically match the simulated population with observed data sources. The stock assessment model incorporated data from 1972 through 2001. These data included information from fishery-dependent sources (commercial hook-and-line, trawl, and trap fisheries, and recreational headboats, charter boats, and private boats) and the fishery-independent MARMAP survey. Data included annual values for total landings by fishery, length and age frequencies by gear, and indices of abundance for the headboat fishery and MARMAP survey. Additional parameters incorporated in the model included natural mortality rate (assumed to be constant over time), gear selectivity for both MARMAP and fishery data, growth (based on the von Bertalanffy growth equation), recruitment (based on a Beverton-Holt recruitment model), and fishing mortality (SAFMC[3]). This model was specified and programed by SEDAR workshop participants using AD Model Builder software (vers. 6.0.3, Otter Research, Sidney, B.C., Canada).

Data modification

To simulate the lack of fishery-dependent information resulting from a moratorium, we omitted length- and age-frequency data used as input for the stock assessment model from commercial and headboat fisheries for the most recent 0, 1, 2, 3, 4, 5, or 6 years (Table 2). Landings, catch per unit of effort, life history parameters, and the model code were not altered. We did not remove landings from the stock assessment model because omitting landings would have changed the estimates of both fishing mortality and biomass, making comparisons of results among models impossible. Therefore, these simulations represent how the lack of fishery-dependent length and age information due to a moratorium would affect assessment results, rather than show the direct effects of reduced fishing mortality on the population. To incorporate stochasticity, we randomly sampled (with replacement) MARMAP length and age frequencies from observed frequencies. For each duration of moratorium (0, 1, 2, 3, 4, 5, and 6 years), we conducted 50 model runs. Results from the stock assessment models, including the status indicators relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}), were compared among simulations. In order to identify differences in variability, we calculated the standard deviation of status indicators among the 50 simulations for each simulated moratorium duration.

Population projections

Output from each of the stock assessment model runs was used as input for population projections to evaluate potential management options according to the method developed during the SEDAR process (SAFMC[3]). Starting with the biomass estimate from the most recent year (as estimated by each stock assessment model), stock projections were run under four potential management scenarios: 1) no fishing mortality or bycatch mortality, as if all fisheries in the region were closed (F=0); 2) fishing mortality under a red porgy moratorium (i.e. where there is only bycatch mortality [F=0.054]); 3) fishing mortality representative of Amendment 9 (F=0.173); and 4) fishing mortality representative of Amendment 12 (F=0.107; Table 1). SEDAR workshop attendees determined fishing mortality rate (F) for each option, and SEDAR projection results are shown in Figure 3 (SAFMC[3]).

The 25-year projections were based on a simulated age-structured population with stochastic stock-recruit relationship and fishing mortality. Initial (2001) stock size-at-age, weight-at-age, annual biomass and recruitment, B_{MSY}, and steepness estimated by the stock assessment model for each model run were used as input for population projections. Other projection input

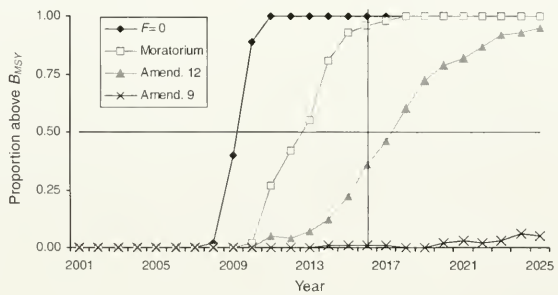

Figure 3

SEDAR population projections for red porgy (*Pagrus pagrus*) under four potential management scenarios. For a management option to be recommended, there must be at least a 50% likelihood (horizontal line) of the population biomass being greater than B_{MSY} before the year 2016 (vertical line).

that remained constant among model runs included natural mortality, maturity at age, and selectivity. Projections for each model run were repeated 100 times for each simulation. The resulting projections allowed us to investigate how data reduction would affect management decisions. For each moratorium length, we estimated the probability of rebuilding success as the proportion of the stochastic runs in which the biomass reached B_{MSY} before the rebuilding deadline of year 2016. For a management option to be recommended, the SAFMC wanted at least a 50% likelihood of the population biomass exceeding B_{MSY} before 2016.

Results

Variability among the simulations increased when multiple years of fishery-dependent length and age data were removed (Fig. 4, and Fig. 5, A and B). When only one or two years of fishery-dependent length and age data were removed, variability and status indicator estimates (such as B/B_{MSY} and F/F_{MSY}) did not differ substantially from simulations where no data were removed. However, when three to six years of fishery-dependent data were omitted, variability increased, especially for F/F_{MSY} (Figs. 4 and 5B). These trends in variability were also evident in population projections, where the range and confidence interval width of projected outcomes increased as data were removed (Fig. 6).

Additionally, removal of data led to higher estimates of population productivity (i.e., higher biomass and faster population rebuilding). When greater than three years of data were removed, projections tended to predict a slightly faster recovery (Figs. 6 and 7). Data availability would have affected management decisions for Amendment 12 because many data-poor models would have incorrectly identified Amendment 12 as a suitable management option (Figs. 6 and 7).

Discussion

Removing data from fishery-dependent sources for multiple years increased the variability of stock status indicators and projections. This variability was amplified during population projections, when the likelihood of rebuilding became increasingly variable as data were removed. Projections are, by nature, uncertain, but this uncertainty increased with even small reductions in information. Similar increases in variance were found by Chen et al. (2003) when information was removed from a New Zealand abalone (*Haliotic iris*) stock assessment model. When Chen et al. (2003) removed fishery-independent length data, standard deviation of parameter estimates increased 33%.

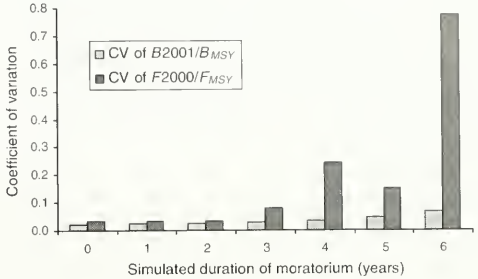

Figure 4

Coefficient of variation (standard deviation among 50 simulations for each moratorium duration divided by the mean) for red porgy (*Pagrus pagrus*) for B_{2001}/B_{MSY} and F_{2000}/F_{MSY}. Fishery-dependent length and age data were removed from the stock assessment model runs for the number of years specified.

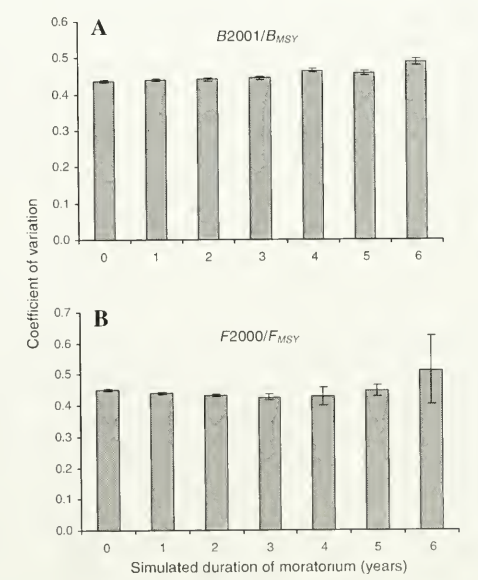

Figure 5

Mean estimates and 95% confidence intervals of (**A**) B_{2001}/B_{MSY} and (**B**) F_{2000}/F_{MSY} for 50 model runs for each moratorium duration for red porgy (*Pagrus pagrus*). Fishery-dependent length and age data were removed from stock assessment model runs for the number of years specified.

In addition to the expected outcome of higher variance as data were removed, we also found a slight tendency toward overestimating stock productivity that resulted from eliminating multiple years of data. When fishery-dependent length and age information were removed, the model tended to predict slightly higher biomass, lower fishing mortality, and faster population recovery. This finding was also supported by Chen et al. (2003), for whom data removal led to a more optimistic estimation of the current fishery status and stock productivity. This bias would increase the potential for overharvesting because the population may not be as productive as the model results suggest. The results of our study are specific to the South Atlantic red porgy stock and may not be applicable to other stocks or species. Stock status indicators and productivity estimates are affected by life history parameters, population size, historical and current fishing pressure, and data availability and these will differ among species. Additionally, use of an alternative stock assessment model could also affect results. However, if this bias is present for other species and stock assessment models, it could have serious implications for managers because it implies that the less information we have on a population, the more productive we would estimate (incorrectly) the population to be.

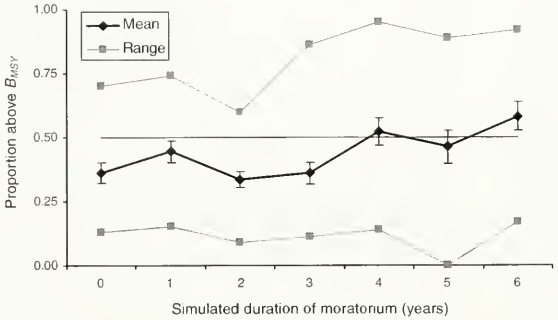

Figure 6

Proportion of projected red porgy *Pagrus pagrus* biomass estimates for the year 2016 under Amendment 12 for which the biomass was greater than B_{MSY}. The mean likelihood for 50 model runs for each moratorium duration is shown (with 95% confidence intervals) and the range of the 50 model runs is shown in gray. For a management option to be recommended, there must be at least a 50% likelihood (horizontal line) of the biomass being above B_{MSY}. Fishery-dependent length and age data were removed from stock assessment model runs for the number of years specified.

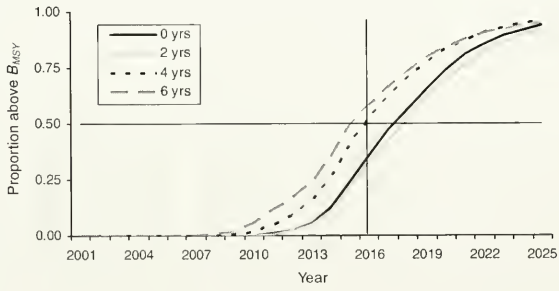

Figure 7

Stock projections (50 model runs for each moratorium duration) under Amendment 12 fishing mortality levels. Fishery-dependent length and age data were removed from stock assessment model runs for the number of years specified. For a management option to be recommended, there must be at least a 50% likelihood (horizontal line) of the population biomass being greater than B_{MSY} before the year 2016 (vertical line).

In general, removing red porgy length and age data had only minor effects on status indicator estimates, projections, or management decisions. The signal of a declining red porgy population was so strong and relatively consistent among data sources that removing a portion of this information did not greatly affect results. All model runs showed an overfished population but one that is not currently undergoing overfishing, and management decisions were also relatively consistent. In all cases, projections showed that rebuilding to B_{MSY} by the year 2016 would occur with no fishing mortality or a moratorium, and fishing mortality representative of Amendment 9 would be insufficient to rebuild the stock. Differences in management decisions did exist for model runs conducted under Amendment 12 fishing mortality levels; some data-poor models incorrectly identified Amendment 12 as a suitable option for rebuilding the stock. For a fish population closer to an overfished status or to a condition where overfishing is in progress, or where data sources were contradictory, data removal could affect stock assessment results and management decisions to a greater extent.

Because red porgy is a well-studied species for which there are 30 years of information from multiple sources, we removed a relatively small proportion of the data used in the stock assessment for our model runs. Conducting these types of simulations on a lesser-studied spe-

cies would most likely result in larger changes in status indicator estimates, projections, and management decisions because a larger proportion of information would be removed. The results of our study on red porgy identified the importance of investigating the potential effects of reducing fishery-dependent information on stock assessment results. If used before implementing management actions, this kind of data simulation study could estimate the potential impact of a lack of data before harvest restrictions are put in place that would cause data loss.

Management implications

These types of simulation studies aid in understanding the impacts of data quantity on stock assessments, particularly with respect to uncertainty and variance. By incorporating uncertainty due to data loss into management decisions, managers will be better able to assess and manage these populations. For example, SEDAR population projections estimated that red porgy required a 12-year moratorium for the population to rebuild to B_{MSY} (Fig. 3). However, our data simulations showed that variability surrounding status indicators increased when as few as three years of fishery-dependent data were removed (Fig. 4) and that a tendency toward overestimating productivity also increased with duration of the moratorium (Fig. 7). Therefore, if managers implemented a 12-year moratorium for red porgy (with no additional sampling), it is possible that a stock assessment conducted at the end of the moratorium would be unable to accurately estimate stock status and identify whether or not the population biomass had reached B_{MSY}.

This study highlights the importance of additional sampling during periods of strict regulations to compensate for the fishery-dependent data that are lost (Olney and Hoenig, 2001). Because many reef fish species are caught in the same fisheries, analysis of bycatch through a fisheries observer program would yield valuable data for a number of species. Another option for data collection would be to initiate a "test fishery" after a moratorium in order to collect fishery-dependent data in a relatively short time and then use these data to estimate stock status. A third option would be to use additional sampling during a moratorium from fishery-independent sources. Although MARMAP data are currently insufficient for assessments of many reef fishes, an expanded survey (i.e., into deeper water, more gear types, etc.) could prove to be valuable in future assessments. Even without a moratorium in place, assessments of many species would undoubtedly benefit from information collected by a fisheries observer program or an expanded fishery-independent survey. Data collected from these sources before a period of strict regulation would improve the ability of scientists to detect trends because a longer time series would make population recovery more apparent than that seen without such data.

The data quantity simulations conducted in our study could also be used for other species. This method allows managers to simulate the effects of a lack of data before enacting regulations or sampling changes that cause data loss. If a loss of information is shown to affect stock assessment results, simulations can be conducted to identify whether additional data will be needed and to test the effectiveness of additional sampling before implementing a sampling program. Stock assessments frequently use population projections to predict the effects of a policy on the stock. Our methodology is an expansion of this idea, using simulations to predict how a policy affects our ability to identify changes in the stock. By incorporating uncertainty due to data loss into management decisions, managers will be better able to assess and manage these populations and improve sampling to better fulfill future research needs.

Acknowledgments

This research was funded by the South Atlantic Fishery Management Council. We thank E. Williams, M. Prager, D. Vaughan, and K. Shertzer for providing modeling advice, J. Potts and P. Harris for information, J. Ney and R. Neves for guidance, and the many state and federal biologists and SAFMC staff members that assisted us in this project. This manuscript was improved by the comments and suggestions of M. Prager and two anonymous reviewers. We greatly appreciate the time and effort of all involved.

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Abstract—The goal of this study was to provide insight into habitat use of the inner continental shelf off southern New Jersey by summer-spawned bluefish (*Pomatomus saltatrix*). Throughout the August–October 1998 sampling period, a total of 1071 bluefish were collected from shelf surface waters, during which the mean density and body size was 3.7 bluefish/1000 m^3 and 13.7 mm standard length (SL), respectively. Spatiotemporal variability in bluefish density was explained by an inverse relationship with Secchi depth, and body size was explained by water temperature and depth. Bluefish size-structure in August was bimodal and comprised larval, transitional, and juvenile stages (3–48 mm SL). Size frequencies in subsequent months were unimodal and consisted of bluefish <25 mm SL. Synoptic sampling of multiple habitats indicated that the earliest life stages of bluefish extensively, and perhaps exclusively, use inner continental shelf surface waters. Summer-spawned bluefish numerically dominated the population across all habitats and temporal scales examined.

Habitat use of the inner continental shelf off southern New Jersey by summer-spawned bluefish (*Pomatomus saltatrix*)*

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Manuscript submitted 14 April 2005 to the Scientific Editor's Office.

Manuscript approved for publication 6 March 2006 by the Scientific Editor.

Fish. Bull 104:593–604 (2006).

Bluefish (*Pomatomus saltatrix*) is a coastal marine species that is common in temperate and subtropical waters worldwide (Juanes et al., 1996). Bluefish support extensive fisheries throughout their distribution (Juanes et al., 1996), including the western north Atlantic where this species has historically accounted for the greatest catch by weight in the recreational fishery (Pottern et al., 1989). Along the eastern coast of the United States, for example, bluefish landings in 1985 contributed to over 24% of the total marine recreational catch (U.S. Department of Commerce, 1986). Since the mid-1980s, however, bluefish landings in this area have declined precipitously and have yet to rebound in the last two decades (Klein-MacPhee, 2002). As a result, the Atlantic States Marine Fisheries Commission (ASMFC) established bluefish as a priority research subject and further recommended that research provide a better understanding of the early life history and recruitment patterns of this species.

Recruitment dynamics of bluefish along the eastern coast of the United States are intrinsically linked to annual spawning migrations of the adult population. Bluefish spawning migrations move northward into the Middle Atlantic Bight (MAB; Cape Hatteras, North Carolina, to Cape Cod, Massachusetts) during the spring and summer following an overwintering period in the South Atlantic Bight (SAB; Cape Canaveral, Florida to Cape Hatteras) (Klein-MacPhee, 2002) or at the edge of the continental shelf in the MAB (Miller, 1969; Wilk, 1982; Shepherd et al., in press). Pelagic eggs are spawned offshore during the spring and summer as bluefish migrate northward along the continental shelf. The planktonic eggs of bluefish experience a brief incubation period (48 hours; Deuel et al., 1966) that is followed by a larval stage that concludes 18–25 days after hatching and once the bluefish are 10–12 mm standard length (SL) (Hare and Cowen, 1994). Bluefish then undergo a transitional period, ending with the

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onset of the juvenile stage at 34–37 mm SL (Silverman, 1975). Juveniles remain oceanic for an additional 15–45 days before passively or actively recruiting to estuarine habitats at 40–80 mm fork length (FL) (Nyman and Conover, 1988; McBride and Conover, 1991; Hare and Cowen, 1993).

Along the U.S. northeastern coast, juvenile bluefish recruit to estuaries and have a consistent intra-annual and bimodal length-frequency distribution: the first cohort enters estuaries from late May to early June (spring-spawned cohort), and a second cohort enters from July to October (summer-spawned cohort) (Nyman and Conover, 1988; McBride and Conover, 1991; McBride et al., 1993; Creaser and Perkins, 1994). This is consistent with previous studies that indicate that juveniles of both spring and summer cohorts are estuarine dependent (Juanes et al., 1996; Able and Fahay, 1998). There is recent evidence, however, that select cohorts of bluefish may exclusively use alternative habitats, such as ocean beaches, during the juvenile stage (Able et al., 2003; Wilber et al., 2003). In addition, samples of larval and juvenile bluefish from surface waters on the inner continental shelf have indicated at least two cohorts of presumably summer-spawned fish that may not recruit to estuaries (Kendall and Walford, 1979; Rowe et al.[1]; Taylor and Able, in press).

Spring-spawned bluefish historically dominate juvenile year-class strength and were therefore assumed to determine adult population dynamics (Nyman and Conover, 1988; McBride and Conover, 1991; Munch and Conover, 2000). This assertion, however, is based primarily on estimates of juvenile abundance in MAB estuaries (Nyman and Conover, 1988; McBride and Conover, 1991) and failed to consider contributions from alternative habitats, including the inner continental shelf. A more recent evaluation of bluefish collected from the MAB also has indicated a shift in the cohort-specific production of juveniles over the last decade (Conover et al., 2003), such that summer-spawned fish numerically dominate recent year classes. Despite the apparent switch in the relative dominance of the two cohorts, bluefish successfully recruiting to the adult population remain the products of spring-spawning events (Chiarella and Conover, 1990; Conover et al., 2003). The factors underlying the apparent failure of the summer-spawned cohort to contribute substantially to the adult population are unknown. This failure is due, in part, to insufficient information that would otherwise enable a critical evaluation of each cohort's role in regulating year-class strength. Attempts to determine factors affecting recruitment patterns should include an evaluation of the cohort dynamics of summer-spawned bluefish that utilize inner continental shelf habitats.

The goal of our study was to provide greater insight into the habitat use by summer-spawned bluefish in a localized area in the MAB. In 1998, young-of-the-year (YOY) bluefish were sampled during the summer and fall on the inner continental shelf off southern New Jersey. Spatial and temporal abundance and distribution patterns were used to evaluate the potential importance of continental shelf waters as habitats for YOY bluefish. Observations from the 1998 study were then analyzed and compared to observations from other field surveys of habitat use by YOY bluefish in the same geographic region and time: inshore and other continental shelf waters of southern New Jersey in 1998 (Able et al., 2003).

Material and methods

Sampling of surface waters over the inner continental shelf

Bluefish were sampled at the water surface along the inner continental shelf off the southern coast of New Jersey (Fig. 1). Specifically, a 4×4 station grid (total area ~825 km^2) was sampled on ten dates between 11 August and 9 October 1998. Stations were grouped into four transects that were aligned parallel to the coastline (Fig. 1A). Transects closest and farthest from the coastline were 3 km and 18 km offshore, respectively. Water depths ranged between 6 and 29 m, and the shallowest depths generally occurred near the shore.

Bluefish were collected during daylight with a Methot trawl deployed at the surface (Methot, 1986; Oozeki et al., 2004). The frame trawl had a mouth area of 5 m^2, leading to an 11-m-long net (6-mm mesh) that tapered to a 2-m-long plankton net (0.5-m diameter, 500-μm mesh). One tow was performed at each of the 16 stations per sampling date, with the exception of 11 August and 9 October when only four and eight stations were sampled, respectively (n=140 total tows). At each station, the trawl was towed for four minutes in an arc (tow speed ~2.5–3.5 knots) to avoid the wake of the research vessel. All tows were made at the surface (0–2 m depth) with the top of the frame approximately 0.25 m out of the water. Samples were immediately processed after collection, and bluefish were preserved in 95% ethanol for subsequent laboratory analysis.

A General Oceanics flowmeter (General Oceanics, Inc., Miami, FL) was attached to the Methot trawl frame along a lower corner so that the volume of water sampled could be determined (~2000 m^3 per tow). Surface salinity, surface water temperature, water depth, Secchi depth, and wind speed and direction were recorded at all stations. Additional wind data were available as a time series (15-minute sampling interval) from a meteorological platform located at the Rutgers University Marine Field Station (Tuckerton, NJ; Fig. 1A; K. W. Able, unpubl. data).

[1] Rowe, P. M., K. W. Able, and M. J. Miller. 2002. Distribution, abundance, and size of young-of-the-year bluefish (*Pomatomus saltatrix*) in ocean and estuarine habitats in southern New Jersey during 1999–2000, 54 p. Jacques Cousteau Technical Report no. 100-16. Rutgers University, Institute of Marine and Coastal Sciences, Marine Field Station, 800 c/o 132 Great Bay Boulevard, Tuckerton, NJ 08087-2004.

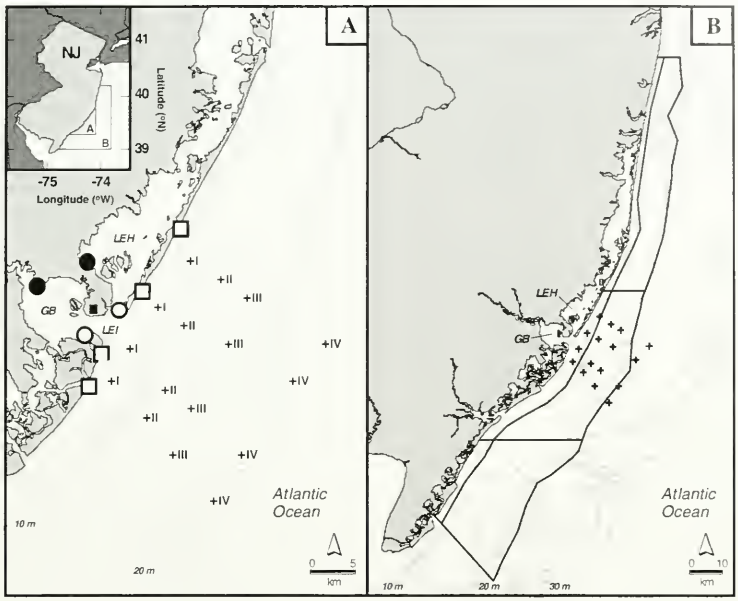

Figure 1

Map of inshore and inner continental shelf habitats off southern and central New Jersey. Plus symbols (✚) demarcate the 4×4 station grid (total area ~825 km^2) sampled with a surface-deployed Methot trawl on the inner continental shelf between 11 August and 9 October 1998. (**A**) Inner continental shelf sampling sites were grouped into four transects (I–IV) aligned parallel to the coastline. Estuarine (●), inlet (○), and ocean beach (□) sites sampled with a beach seine were located at the margins of Great Bay (GB), Little Egg Harbor (LEH), and Little Egg Inlet (LEI). (**B**) Solid lines (—) demarcate six depth strata sampled with an otter trawl on the inner continental shelf. Location of the Rutgers University Marine Field Station (Tuckerton, NJ; ■) and depth contours of 10, 20, and 30 m are provided.

Bluefish collected with Methot trawls were counted to estimate fish density (no. of bluefish/1000 m^3), measured to the nearest mm SL, and classified into distinct ontogenetic stages based on the individual's body size and presumed scale development (Silverman, 1975; Able and Lamonaca, in press). For the purposes of our investigation, several life history stages were demarcated: larval, transitional, and juvenile. The onset of scale development was recognized as the end of the larval stage and the beginning of the transitional period (12 mm SL; Silverman, 1975; Hare and Cowen, 1994). The transitional period in bluefish development, in turn, concluded with complete scale formation and the juvenile stage began at 34 mm SL (Silverman, 1975).

Spatial and temporal patterns of bluefish density and mean size were analyzed independently with multivariate repeated-measures analysis of variance (ANOVA) models by using station transects (transects I–IV; Fig. 1A) and sampling date (day of year) as the between-subject and within-subject factors, respectively. Profile transformation of the within-subject factor was used in the repeated-measures ANOVA model, and statistical significance was estimated from the Greenhouse-Geisser–adjusted probability to avoid violating the assumption of circularity (sphericity) of the within-subject variance-covariance matrix (von Ende, 1993). The mean density and body size of bluefish across four levels of transects and ten levels of sampling dates were contrasted with a Ryan-Einot-Gabriel-Welsch (Ryan's Q) multiple comparison test (Day and Quinn, 1989). Moreover, natural log $(x+1)$ and natural log (x) transformations were performed on bluefish density and mean-size data, respectively, to meet assumptions of normality and homogeneity of variance. When data transformations did not achieve homoscedasticity, hypotheses were rejected at alpha values lower than the P-values of Levene's test for homogeneity of variance (Underwood, 1981).

The effects of several environmental parameters on the spatial and temporal distribution of bluefish density and mean size were analyzed with a stepwise multiple regression. The variables included in the regression

Table 1

Summary of field sampling protocols, habitat characteristics, and bluefish (*Pomatomus saltatrix*) catch and size data across multiple areas of southern and central New Jersey in the summer and fall of 1998. Bluefish catch data are reported as catch per unit of effort (CPUE). Temperature, salinity, and size data within parentheses represent minimum and maximum values observed on a given date, and NM and NA signify "no measurement" and "not applicable," respectively. Additional information regarding habitat location and sampling protocols is found in the text and Figure 1.

Habitat	Sampling gear	Sampling effort (no. of tows)	Depth (m)	Temperature (°C)	Salinity (‰)	CPUE (no. per tow)	Size (mm SL)
Continental shelf (surface waters)							
11–20 Aug 1998	Methot trawl	68	6–28	25.5 (16.5–27.3)	30.7 (30.0–31.1)	4.4	18.7 (3–48)
1–11 Sep 1998	"	32	6–29	24.0 (21.8–25.5)	30.6 (30.3–30.7)	2.3	10.1 (5–25)
18–25 Sep 1998	"	32	6–27	22.5 (21.0–23.6)	30.7 (30.3–31.0)	21.7	12.0 (4–24)
6 Oct 1998	"	8	9–29	19.5 (18.7–20.3)	30.7 (30.6–30.9)	0.6	18.7 (18–22)
Estuary							
13–24 Aug 1998	Beach seine	8	0–2	25.0 (24.0–26.0)	28.5 (28.0–29.0)	0.3	116.0 (60–172)
9 Sep 1998	"	5	"	19.9 (19.5–20.5)	28.0 (28.0–28.0)	0.4	111.0 (104–118)
21 Sep 1998	"	5	"	27.0 (27.0–27.0)	NM	0.2	116.0
5 Oct–3 Nov 1998	"	15	"	16.0 (10.5–19.0)	27.8 (26.0–29.0)	0.1	147.0
Inlet							
4–21 Aug 1998	Beach seine	9	0–2	25.7 (25.0–26.0)	29.3 (28.0–30.0)	3.3	83.1 (59–103)
3–4 Sep 1998	"	5	"	25.6 (25.0–26.0)	28.8 (28.0–30.0)	4.0	78.9 (55–113)
14–29 Sep 1998	"	10	"	21.7 (20.0–23.0)	29.7 (29.0–30.0)	0.5	96.2 (91–99)
13–29 Sep 1998	"	12	"	15.0 (13.0–17.0)	29.3 (29.0–30.0)	0.0	NA
Ocean beach							
3–25 Aug 1998	Beach seine	32	0–2	25.4 (23.0–27.0)	30.1 (28.0–31.0)	14.1	73.3 (51–168)
2–8 Sep 1998	"	16	"	24.4 (23.0–26.0)	30.4 (30.0–31.0)	53.7	76.5 (53–123)
14–30 Sep 1998	"	26	"	22.6 (20.0–26.0)	30.1 (29.5–31.0)	50.2	96.6 (27–205)
6 Oct–4 Nov 1998	"	41	"	15.6 (13.0–18.0)	30.0 (30.0–30.0)	93.2	118.5 (32–225)
Continental shelf (bottom)							
17–20 Aug 1998	Otter trawl	17	6-18	19.6 (12.3–25.4)	30.9 (28.3–31.5)	10.5	63.8 (30–200)
30 Oct–4 Nov 1998	"	17	"	14.4 (12.6–15.4)	31.4 (30.1–31.9)	21.6	125.6 (80–220)

model were sampling date (day of year), sampling time of day (sine-transformed), station distance from coastline (km), surface temperature (°C), surface salinity (‰), Secchi depth (m; a coefficient of light extinction or water clarity), water depth (m), and cross- and long-shelf wind speed (positive east and north, respectively). The significance level for entry into the regression model was set at $P<0.05$. Environmental variables that significantly affected the spatial and temporal distribution of bluefish density and mean size (i.e., those parameters incorporated into regression models) were also analyzed with an analysis of covariance (ANCOVA) model, with sampling date as the covariate and station transects as the discrete explanatory variable.

Synoptic analysis of habitat use by summer-spawned bluefish

Several other sampling programs initiated in 1998 monitored the distribution and size composition of YOY bluefish across multiple habitats in southern and central New Jersey (Table 1, Fig. 1) and the data from these programs were then compared to our data from surface waters on the inner continental shelf. A complete description of the sampling protocols and schedules for monitoring YOY bluefish in these habitats is provided elsewhere (Able et al., 2003; Rowe et al.[1]). Habitat use by different ontogenetic stages was ascertained from the size and stage (larval, transitional, juvenile) composition of bluefish observed in estuaries, inlets, ocean beaches, and the inner continental shelf. Accordingly, length-frequency histograms of bluefish were created for each habitat over four time periods (August, early to mid-September, mid-to-late September, and from October to November) by using class intervals of 5.0 mm SL for Methot trawl and beach seine samples, and 10.0 mm SL intervals for otter trawl samples. Moreover, a length-based key derived by McBride and Conover (1991) and adopted by others (Juanes and Conover, 1995; Wilber et al., 2003) was used to delineate between spring- and summer-spawned

bluefish in length-frequency histograms. Summer-spawned bluefish were defined as <100 mm SL in August, <125 mm SL from early to mid-September, <150 mm SL from mid-to-late September, <175 mm SL from October to November. Bluefish at body sizes larger then these groupings were designated as spring-spawned individuals.

Results

Bluefish density and mean size on the inner continental shelf

A total of 1071 bluefish were collected from surface waters off the southern coast of New Jersey during the survey. Throughout the August–October sampling period, bluefish were found in 71% of the tows (99 out of 140), during which the mean density was 3.7 bluefish/1000 m^3 (range=0–57.9 bluefish/1000 m^3). Bluefish density differed significantly by transect and sampling date (multivariate repeated-measures ANOVA; transect: $F=9.39$, df=3,12, $P<0.005$; date: $F=16.09$, df=9,88, $P<0.0001$). However, the transect-sampling date interaction effect was significant and precluded direct conclusions about the main effects (multivariate repeated-measures ANOVA; transect × date: $F=1.95$, df=27,88, $P<0.05$) (Fig. 2). The interaction effect was attributed to significantly higher densities of bluefish at transect II on days 226 and 268 (in comparison to transects I, IV, and transect I on these days, respectively (Ryan's Q multiple comparison test). Bluefish densities were also significantly greater at transect III on days 226 and 244 than at transect I for both dates (Ryan's Q multiple comparison test).

In the stepwise multiple regression, Secchi depth explained the most variability in bluefish density with an r^2 of 0.078 (stepwise multiple

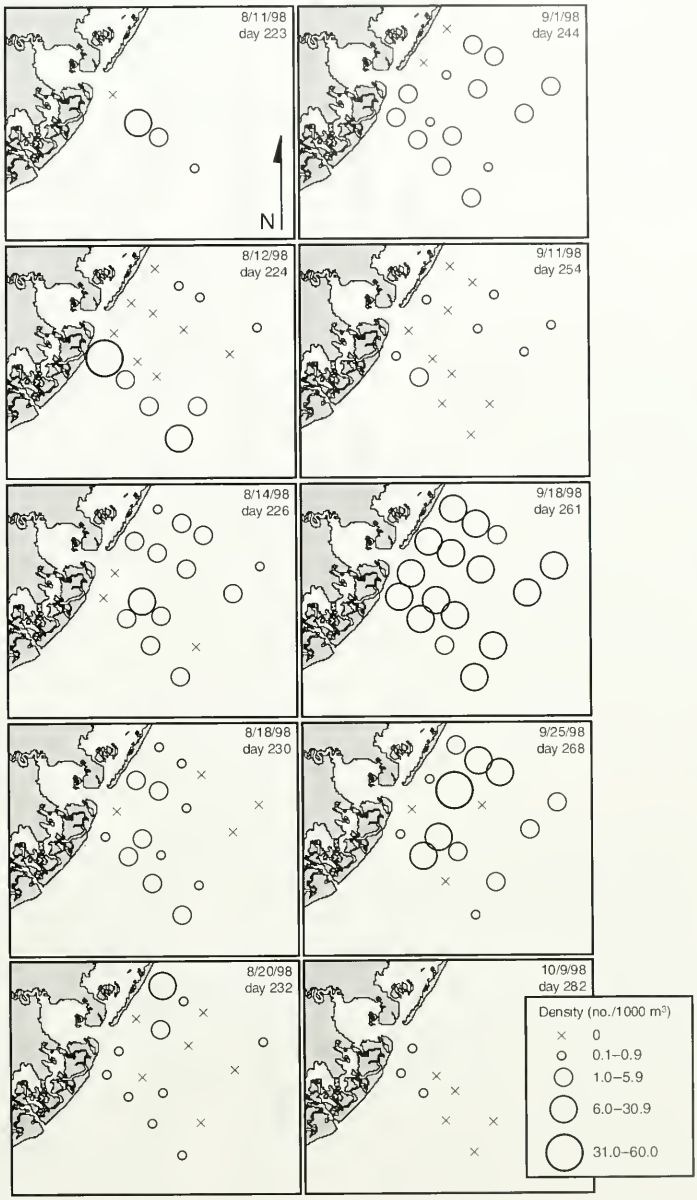

Figure 2

Spatial distribution of the density (no. of fish/1000 m^3) of bluefish (*Pomatomus saltatrix*) collected with a Methot trawl between 11 August and 9 October 1998 off the southern coast of New Jersey. Stations were located at approximately 39°27'N, 74°11'W.

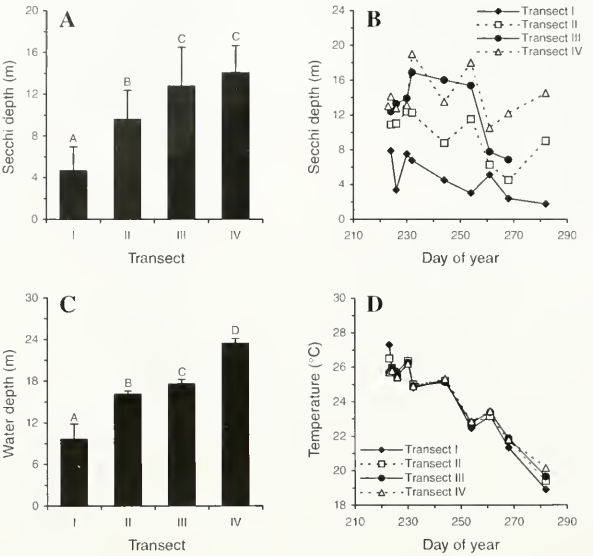

Figure 3

Spatial and temporal distribution (**A** and **B**) of Secchi depth (m), (**C**) water depth (m), and (**D**) surface water temperature (°C). Mean (±1 standard deviation) Secchi depth and water depth are displayed as a function of station transects (I–IV; Fig. 1A), calculated from ten sampling dates between 11 August and 9 October 1998 (days 223–282). Means with the same upper case letters are not significantly different (Ryan's Q multiple comparison test). Secchi depth and surface water temperature are also displayed as function of station transects and sampling date (days 223–224).

regression; F=11.34, df=1,135, P<0.001), and remaining parameters were not significant at P<0.05 and therefore not included in the model. The estimated coefficient for Secchi depth was negative (parameter estimate=−0.436), indicating an inverse relationship between bluefish density and water clarity. Before analyzing spatial and temporal variations in Secchi depths with an ANCOVA model, we examined the interaction effect between transect and sampling date. There was no significant transect-date interaction effect (two-way ANOVA; transect×date: F=2.47, df=3,124, P=0.065), and the assumption of equal slopes was met in the full data set (Underwood, 1981). Secchi depth differed significantly as a function of transect position (ANCOVA; F=63.34, df=3,127, P<0.0001), whereby distance from the coastline was positively correlated with Secchi depth (Fig. 3A). Furthermore, Secchi depth significantly decreased throughout the sampling period (ANCOVA; F=30.20, df=1,127, P<0.0001) (Fig. 3B).

The mean body size of bluefish collected from August to October was 13.7 mm SL (range=3–48 mm SL) (Table 1; Fig. 4). Similar to spatial and temporal density patterns, bluefish mean body size differed significantly by transect and sampling date (multivariate repeated-measures ANOVA; transect: F=6.16, df=3,12, P<0.01; date: F=7.50, df=9,50, P<0.0001) (Fig. 4). The transect-sampling date interaction effect was again significant (multivariate repeated-measures ANOVA; transect×date: F=3.50, df=24,50, P<0.0001), thereby precluding contrasts across main effects. The interaction effect was caused by significantly larger bluefish at transects I and II on day 254 compared to transects III, IV, and transect III, respectively (Ryan's Q multiple comparison test). On day 268, significantly larger bluefish were collected at transect IV than at all other transects (Ryan's Q multiple comparison test).

Surface water temperature and water depth were the most significant factors affecting the size distribution of bluefish (stepwise multiple regression; temperature: F=14.07, df=2,94, P<0.0005; depth: F=5.50, df=2,94, P< 0.05), such that temperature and depth accounted for a partial r^2 of 0.129 and 0.048, respectively (cumulative r^2=0.177). Moreover, estimated coefficients for both variables were negative (parameter estimates=−1.121

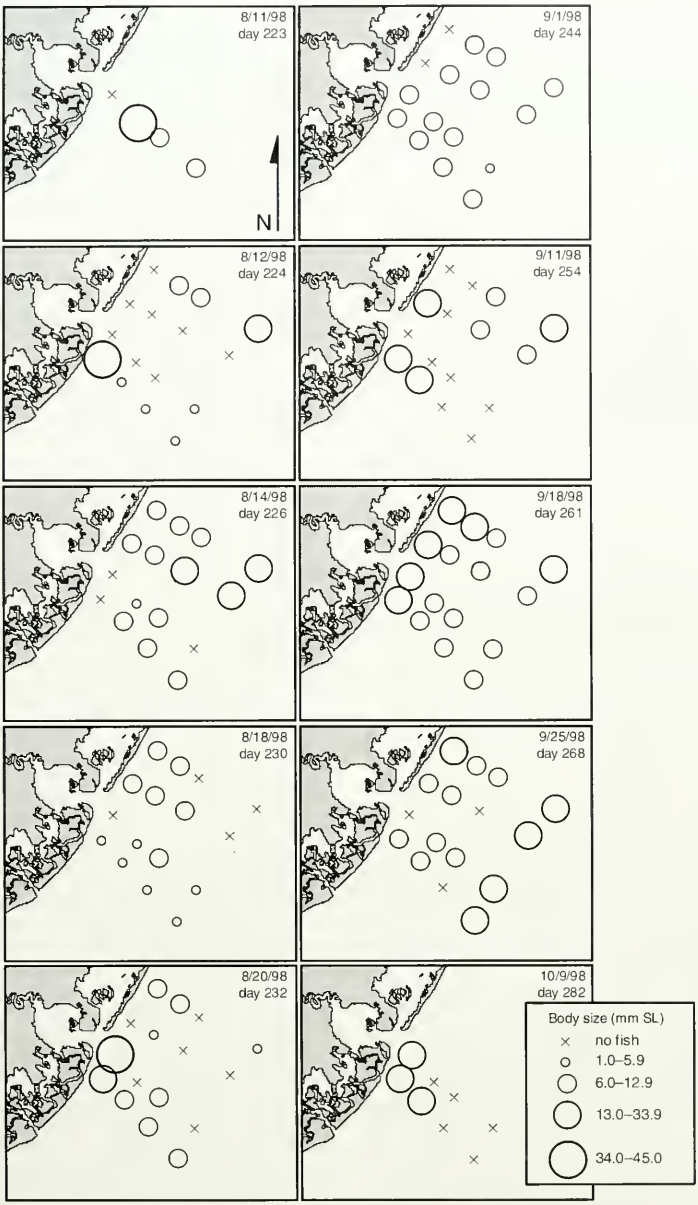

Figure 4

Spatial distribution of the mean size (mm SL) of bluefish (*Pomatomus saltatrix*) collected with a Methot trawl between 11 August and 9 October 1998 off the southern coast of New Jersey. Stations are located at approximately 39°27'N, 74°11'W.

and −0.254 for temperature and depth, respectively) indicating that larger bluefish were associated with relatively cool surface water and shallow water depths. Before analyzing spatial and temporal variations in temperature and depth with an ANCOVA model, we examined the transect-sampling date interaction effect. There were no significant interactions between transect and date for both analyses (two-way ANOVA; depth–transect×date: F=0.72, df= 3,132, P=0.5401; temperature–transect×date: F=1.87, df=3,132, P=0.1385). Water depth significantly increased as distance from the coastline increased (ANCOVA; F=231.24, df=3,135, P<0.0001) (Fig. 3C), and surface temperature significantly decreased during the sampling period (ANCOVA; F=916.49, df=1,135, P<0.0001) (Fig. 3D).

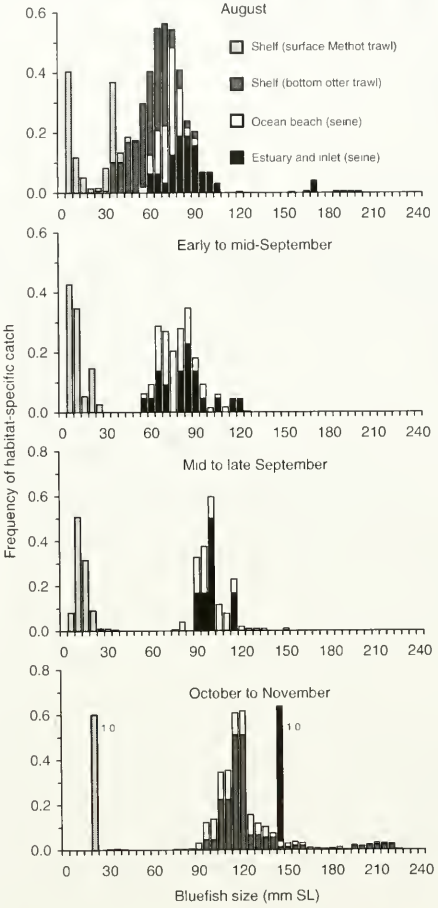

Figure 5

Composite length-frequency histograms for bluefish (*Pomatomus saltatrix*) collected from multiple habitats in summer and early fall (1998) in southern and central New Jersey. Additional information regarding habitat location and sampling protocols is found in the text, Table 1, and Figure 1.

Transitional bluefish (25–34 mm SL) and juveniles (35–50 mm SL) were a major portion of the overall size composition of bluefish collected in August (Fig. 5). For example, bluefish 25–50 mm SL constituted 40.1% of the individuals collected during this time period. In subsequent months, however, these bluefish were absent from remaining survey tows. Conversely, larval bluefish (3–11 mm SL) and small transitional bluefish (12–24 mm SL) were collected on all sampling dates and were numerically dominant in August and thereafter (Fig. 5). From August to late September, length-frequency distributions of bluefish <25 mm SL generally broadened in range and shifted to larger body sizes.

Synoptic analysis of habitat use by summer-spawned bluefish

Bluefish abundance and size-structure were compared among diverse inshore and coastal habitats in an effort to provide a more synoptic examination of summer habitat use across ontogenetic stages. In the process, bluefish were examined from shallow estuarine, inlet, and ocean beaches to surface and deeper waters on the inner continental shelf. As previously discussed, all individuals collected by Methot trawl tows from shelf surface waters were <50 mm SL, and therefore defined as summer-spawned larval, transitional, or juvenile bluefish (Fig. 5).

Bluefish catches in the Great Bay estuary were low; 33 seine hauls collecting five bluefish from August to October (0.1–0.4 bluefish/haul) (Table 1). With the exception of one bluefish, all individuals in the estuary were designated as summer-spawned fish (Fig. 5). Relatively few bluefish were collected in seine hauls at inlet sites located at the margin of Little Egg Inlet (55 bluefish from 36 hauls) that were primarily summer-spawned (Table 1; Fig. 5). In contrast to estuarine and inlet sites, substantial numbers of bluefish were collected from August to early November along ocean beaches north and south of Little Egg Inlet (6440 bluefish from 115 hauls) (Table 1). Spring-spawned bluefish were consistently collected along ocean beaches during the survey, but abundances were low compared to those of summer-spawned individuals that represented 98.4% of the total catch (Fig. 5). Compared to the sizes of bluefish collected from surface waters of the inner continental shelf, the sizes of the overwhelming majority (99.4%) of fish collected at inshore sites (estuary, inlet, and ocean beaches) were >50 mm SL (i.e., the sizes of juvenile fish). The only exception to this pattern occurred along ocean beaches from mid-September to early November (Fig. 5).

Sampling of bottom waters on the inner continental shelf during the same time period collected 179 and 367 bluefish in August and October–November, respectively (Table 1; Fig. 5). The size composition of bluefish collected from otter trawl tows was comparable to that observed at inshore sites (particularly ocean beaches), but distinctly different from that of fish captured in continental shelf surface waters. For example, 96.5% of the bluefish captured during sampling of shelf bottom waters were >50 mm SL (mean size=63.8 and 125.6 mm SL in August and October–November, respectively). Of the remaining individuals that were <50 mm SL, all were collected during the August otter trawl survey. Spring-spawned bluefish were collected in August and October–November by otter trawl tows, but again these bluefish represented a small portion of the total sampled population (5.1%).

Discussion

In our study, summer-spawned larval, transitional, and juvenile bluefish used the inner continental shelf extensively and represented a major portion of the entire fish assemblage collected in surface waters off the southern coast of New Jersey. For example, summer-spawned bluefish were the most frequently encountered species within the surface fish assemblage and ranked fourth in numerical dominance during the summer and early fall. Moreover, patterns of bluefish density observed in this study are consistent with those seen in other ichthyoplankton surveys in the MAB. Kendall and Walford (1979) found that bluefish larvae <4 mm SL were widely distributed in the MAB in August (Long Island, New York, to Virginia) and that peak concentrations occurred on the inner continental shelf in the vicinity of New Jersey and Delaware. Similarly, Smith et al. (1994) observed high densities of bluefish eggs in June and July and that centers of abundance occurred in mid-shelf waters off Delaware Bay and New Jersey (Berrien and Sibunka, 1999). Subsequent months were characterized by relatively broad spatial distributions of bluefish larvae from the central MAB to southern New England and by dense concentrations off New Jersey in July and August, followed by decreased abundance over the entire continental shelf in October (Kendall and Walford, 1979; Smith et al., 1994). These observations from the inner continental shelf, in conjunction with the reported use of inshore habitats by summer-spawned juveniles (McBride and Conover, 1991; Able et al., 2003; Wilber et al., 2003), indicate that coastal regions of New Jersey and adjacent areas are important summer-spawning sites for bluefish and, moreover, represent an appropriate location for synoptic comparisons of bluefish abundance and size-structure across habitats.

Empirical observations indicate that summer-spawned bluefish may use inner continental shelf habitats and, to a lesser extent, ocean beaches during their earliest life history stages (larval, transitional, and small juveniles). As surmised from this and previous studies, bluefish <50 mm SL are prominent constituents of the ichthyoplankton assemblage in the MAB (Kendall and Walford, 1979; Hare et al., 2001), but the these life stages are found rarely in estuaries and inlets. Field collections from our study indicated an abundant supply of larval to small juvenile bluefish in the vicinity of Little Egg Inlet from August to October, yet these particular life stages were not observed during concurrent sampling at estuarine sites. Moreover, larval fish assemblages were monitored over 16 years (1989–2004) inside Little Egg Inlet (Fig. 1), and bluefish were found in only 0.8% of the total 640 plankton tows performed between July and September (25 total bluefish, size range: 7.6–57.0 mm SL) (Witting et al., 1999; K. W. Able, unpubl. data).

In another study, juvenile bluefish were conspicuous members of the pelagic fish assemblage in Great Bay (Fig. 1), ranking fifth in frequency of occurrence and tenth in numerical dominance (Hagan and Able, 2003). The mean body size of bluefish collected in Great Bay, however, was 87.4 mm FL—a size that indicates that bluefish may not use estuaries during the earliest life history stages. More likely, YOY bluefish recruit to estuarine and ocean beach habitats as small juveniles (40–80 mm FL), as has previously been reported (McBride and Conover, 1991; Hare and Cowen, 1993; Able et al., 2003). This assertion was reconfirmed in our study by the synoptic examination of summer-spawned bluefish across multiple habitats, where the smallest bluefish collected in estuarine, inlet, and ocean beaches averaged 47.3 mm SL.

In contrast to the size-composition of bluefish inhabiting estuarine and coastal ocean sites, bluefish in surface waters on the inner continental shelf were strictly larval, transitional, and small juveniles <50 mm SL (Fig. 5). The paucity of juvenile bluefish >50 mm SL off the southern coast of New Jersey may be attributed to several factors including gear avoidance, size-dependent depth and habitat distributions, and active or passive emigration. First, gear avoidance appears unlikely because of the speed (~2.5–3.5 knots), duration (4 minutes), and frequency (140 tows) at which tows were performed (Norcross et al., 1974). For example, the approximate swimming speed of a 50-mm bluefish is 10 cm/s (Olla et al., 1985; Hare and Cowen, 1993) under the assumption that the fish swims at 2 body length/s (Hunter, 1981). At this rate, it is improbable that juvenile bluefish could actively avoid a Methot trawl being towed at 128–180 cm/s (1 knot=51.44 cm/s). Secondly, larval-to-juvenile bluefish are surface oriented (0–6 m), as indicated by collection efforts across different water depths (Norcross et al., 1974; Kendall and Walford, 1979; Kendall and Naplin, 1981; Shima, 1989) and by morphometric characteristics (e.g., silver and dark blue counter-coloration) of pelagic juveniles that indicate that they are adapted for a surface oceanic existence. Sampling in our study, however, was limited to the immediate surface layer (0–2 m), and therefore the current sampling design would not detect size-dependent depth distributions >2 m. In Virginian coastal

waters, Norcross et al. (1974) did not collect bluefish >22 mm total length in near-surface waters and attributed the absence of this fish to a lack of samples at depths where larger bluefish were presumably concentrated. In our study, continental shelf bottom waters were sampled with otter trawls (trawl vertical opening ~2 m), and the size of first occurrence was 30 mm SL. This finding indicates that juveniles may seek deeper water as body size increases and swimming ability improves (Norcross et al., 1974). Alternatively, small bluefish collected with otter trawl tows may have been concentrated in surface waters and were incidentally captured during initial gear deployment and final retrieval (i.e., under conditions when the otter trawl was inadvertently fishing the upper water column). Third, recruitment of juvenile bluefish >50 mm SL to estuarine or coastal habitats is another plausible explanation for their absence in continental shelf waters. As previously mentioned, bluefish actively or passively migrate inshore at 40–80 mm FL (McBride and Conover, 1991; Able et al., 2003). The size at which bluefish enter inshore habitats may be the result of biological timing and morphological constraints. These two factors are consistent with the fact that inshore recruitment co-occurs with a switch in diet from copepods to available piscine prey (Marks and Conover, 1993; Juanes and Conover, 1995). Correspondingly, bluefish may not enter estuaries until swimming ability improves and morphological development is complete, i.e., when fin ray development and scale formation (between 34 and 37 mm SL) are complete (Silverman, 1975). Swimming ability in many fish species dramatically improves after the transformation from larval to juvenile stages (Hunter, 1981; Stobutzki and Bellwood, 1994). If morphological development is coupled with improved swimming ability in bluefish, juveniles most likely have the physical ability to actively recruit to estuarine habitats from inner continental shelf waters (Shima, 1989; Hare and Cowen, 1993, 1996). This study provides cursory evidence that summer-spawned juveniles move inshore during August and early September. Furthermore, the disappearance of bluefish of 25–50 mm SL from continental shelf surface waters coincided with the appearance of somewhat larger fish (~50–60 mm SL) at estuarine and coastal ocean sites in late August and early September.

Along the northeastern coast of the United States (Cape May, New Jersey, to Long Island, New York), ingress of juvenile bluefish to inshore habitats presumably occurs as two distinct episodes (McBride and Conover, 1991 and references therein); which are consistent with intra-annual and bimodal length-frequency distributions. This bimodality in bluefish size-composition is a result of a first cohort recruiting inshore from late May to early June (spring-spawned cohort), and a second cohort entering the same geographic region from July to October (summer-spawned cohort) (Nyman and Conover, 1988; McBride and Conover, 1991; McBride et al., 1993). In our study, the size-composition of bluefish across habitats was multimodal, yet length-based information indicated that the overwhelming majority of YOY bluefish had been summer-spawned. Similarly, recent investigations of the inshore and continental shelf regions of the MAB also documented the numerical dominance of summer-spawned bluefish in late summer and early fall (Able et al., 2003; Conover et al., 2003; Wilber et al., 2003).

Although summer-spawned bluefish presumedly dominated the catches of YOY across all habitats and temporal scales examined in our study, the recruitment success and contribution of these cohorts to year-class strength is unknown. The abundance of these fish, compared to that of spring-spawned individuals, implies that they potentially make important contributions to bluefish year-class strength (Able et al., 2003); yet it is unknown whether the area sampled in this survey is indicative of bluefish abundance along other portions of the U.S. northeastern coast or whether this survey is representative of other years. Moreover, bluefish spawned later in the season (e.g., those encountered on the shelf in late September and October) may not achieve a size permitting either movement into estuaries or successful seasonal migrations. These bluefish, along with relatively small juveniles, may fail to contribute to the adult population because of size-selective mortality and decreased survival during overwintering periods (Hare and Cowen, 1997; Sogard, 1997; Hales and Able, 2001). There is also a consensus that spring-spawned juveniles frequently dominate the emigrating population in the fall, and therefore, are the key contributors to year-class strength (Nyman and Conover, 1988; Chiarella and Conover, 1990; Munch and Conover, 2000). This assertion has been recently contested, however, because other studies have indicated that summer-spawned bluefish contribute equally, if not exceedingly, to the YOY population (Able et al., 2003; Conover et al., 2003; Wilber et al., 2003). It is probable that bluefish population dynamics along the coastal United States are a function of the combined recruitment success of spring- and summer-spawned cohorts and that contributions vary annually or over decadal scales (McBride and Conover, 1991; Munch and Conover, 2000). As a result, future research must focus on broad geographical areas over sufficiently long temporal periods in order to adequately resolve the contribution of the different bluefish cohorts.

Acknowledgments

We are grateful to the staff of the Rutgers University Marine Field Station for assistance in field collections and processing of bluefish samples, particularly Geoff Bell, David Bottinelli, Ryan Nichols, and Rob Rinaldi. We also thank Doug Clarke (U.S. Army Corps of Engineers) for access to bluefish data from nearshore ichthyoplankton surveys. This study was funded through the Bluefish/Striped Bass Research Program, Rutgers University and National Marine Fisheries Service collaborative program.

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Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf

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Abstract—Longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*) squids are considered important prey species in the Northwest Atlantic shelf ecosystem. The diets of four major squid predators, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*), were examined for seasonal and size-based changes in feeding habits. Summer and winter, two time periods largely absent from previous evaluations, were found to be the most important seasons for predation on squid, and are also the periods when the majority of squid are landed by the regional fishery. Bluefish >450 mm, silver hake >300 mm, and summer flounder >400 mm were all found to be significant predators of squid. These same size fish correspond to age classes currently targeted for biomass expansion by management committees. This study highlights the importance of understanding how squid and predator interactions vary temporally and with changes in community structure and stresses the need for multispecies management in the Northwest Atlantic.

Manuscript submitted 7 November 2005 to the Scientific Editor's Office

Manuscript approved for publication 9 March 2006 by the Scientific Editor.

Fish. Bull. 104:605–615 (2006).

Global depletion of marine predators has had dramatic effects on ecosystem structure and function (May et al., 1979; Jackson et al., 2001; Pauly et al., 2002). In many systems, the ramifications of such changes may not be fully realized. Groundfish declines have been linked to simultaneous increases in cephalopod landings in fifteen key Food and Agriculture Organization of the United Nations (FAO) areas (Caddy and Rodhouse, 1998). It is uncertain whether cephalopod populations are experiencing increased growth due to a release from predation (Piatkowski et al., 2001), or whether increased harvests are representative of the trend toward fishing species at lower trophic levels (Pauly et al., 1998). In the Northwest Atlantic, while gadids, flatfish, and other demersal species have been reduced because of overfishing (Link and Garrison, 2002), squid have risen in status from a mere bait fishery to one of the most economically important stocks in the region (Cadrin and Hatfield[1]).

Cephalopods have been documented as principal prey for numerous species of finfish, elasmobranchs, and marine mammals (Smale, 1996); however, in comparison to the ecological relationships between fish and their predators, less is known about the ecological interactions between squid and their predators. In a comprehensive evaluation of the Northwest Atlantic food web, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) were ranked among the most significant predators of squid (Bowman et al., 2000). Squid represented between 17% and 95% of the total mass consumed by these four finfish regionally. Dramatic changes in stock abundance and population structure have occurred since specimens for Bowman et al.'s study were collected 25–45 years ago. Exploitation of squid has risen substantially, and the four noted predators have experienced severe depletions; stock biomass levels have fallen as low as 20–50% of their respective maximum sustainable yield (B_{MSY}) limits (NOAA[2]). Additionally, the size structure of predator populations within the community has become skewed because of age-truncation. Recent evaluations of bluefish (Buckel et al., 1999a), goosefish (Armstrong et al., 1996), silver hake (Bowman, 1984), and summer flounder (Link et al., 2002) foraging habits have been conducted; however, sampling has been restricted to one or two seasons, primarily spring and fall. Analyses that base their results on feeding habits collected during a single season (Buckel et al., 1999b), or where results are based on data that have been pooled under the as-

[1] Cadrin, S. X., and E. M. C. Hatfield. 1999. Stock assessment of inshore longfin squid *Loligo pealeii*. Northeast Fish. Sci. Cent. Ref. Doc. 99-12, 107 p.

[2] NOAA (National Oceanic and Atmospheric Administration). 2001. Northeast Fisheries Science Center (NEFSC). Status of fishery resources off the northeastern United States. Website: http://www.nefsc.noaa.gov/sos/spsyn/species.html [accessed on 8 March 2006].

sumption that the diets collected in one season are a proxy for another (Overholtz et al., 2000) could overlook key periods of predation and lead to an underestimation of the total predatory demand imposed on principal prey resources, such as squid.

The two primary squid species found in Northwest Atlantic waters, longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*), are both highly migratory, and their distribution on the shelf is temporally variable. Squid move between inshore (spring and summer) and offshore (fall and winter) environments seasonally (Macy and Brodziak, 2001). On a diurnal basis they move from demersal waters during the day to surface waters at night (Lange and Sissenwine, 1983). The degree of vertical movement made by squid is also known to vary seasonally. Activity is more pronounced during warmer months when the water column is stratified and is diminished during winter and spring when shelf waters are well mixed (Hatfield and Cadrin, 2002). Prey availability and distribution in the water column, water temperature, and other environmental factors are believed to influence diel migration patterns (Cargnelli et al., 1999). Seasonal changes in squid behavior and habitat use will also affect encounter rates with different predators in the demersal environment.

Knowledge of species interactions is imperative to understand population dynamics and to manage stock recovery (Murawski, 1991). The present study provides a current assessment of the reliance on squid populations in the Northwest Atlantic region by four major squid predators; bluefish, goosefish, silver hake, and summer flounder. For each predator, ontogenetic and seasonal variations in feeding patterns were evaluated. Additionally, squid abundance in the demersal environment was related to predator diets as a mechanism for diurnal and seasonal changes in predation.

Materials and methods

Estimating changes in the abundance of longfin inshore squid

Longfin and shortfin squid are regularly caught in National Marine Fisheries Service (NMFS) bottom trawl surveys. However, catches of shortfin squid were exceptionally low over 2002 and 2003 (the time period evaluated during the present study), possibly because of poor recruitment. Catch data used in subsequent calculations were provided by NMFS bottom-trawl surveys (NMFS[3,4,5,6,7,8]). Sufficient information was available for longfin squid only; consequently abundance estimates were limited to this species. Furthermore, abundance surveys were not conducted during the summer; therefore adequate information was not available to evaluate this season.

To compare changes in longfin squid abundance in the demersal environment at different times of day and between seasons, the relative masses of prerecruits (W_P) and recruits (W_R) present were estimated by using the equations

$$W_{P(year,\,season,\,time\,of\,day)} = \sum_t \frac{W_t P_{t(year,\,season,\,time\,of\,day)}}{f_{t(season,\,time\,of\,day)}} \quad (1)$$

$$W_{R(year,\,season,\,time\,of\,day)} = \sum_t \frac{W_t R_{t(year,\,season,\,time\,of\,day)}}{f_{t(season,\,time\,of\,day)}} \quad (2)$$

where t = the index of tows made at NMFS stations in New York, New Jersey, Connecticut, Rhode Island, and Massachusetts respective to each year (2002, 2003), season (winter, spring, fall), and time of day (day, night, dawn and dusk);

W_t = the total mass of longfin squid caught in each tow; and

P and R = $(1 - P)$ estimate the proportion of biomass in each of two size classes, prerecruits (≤80 mm) and recruits (>80 mm), of longfin squid during each season.

f_t = the diel correction coefficient representing relative catch rates of longfin squid for each size class, season, and time of day as determined by Hatfield and Cadrin (2002) and was standardized to 1.0 during daytime for all seasons.

[3] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–SE Georges Bank: February 5–March 2, 2002, FRV *Albatross IV*, 24 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[4] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–Gulf of Maine: March 5–April 25, 2002, FRV *Albatross IV*, 34 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[5] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–Gulf of Maine: September 4–October 25, 2002, FRV *Albatross IV*, 31 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[6] NMFS (National Marine Fisheries Service). 2003. Resource survey report: bottom trawl survey, Cape Hatteras–Southern New England: February 4–March 1, 2003, FRV *Delaware II*, 19 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[7] NMFS (National Marine Fisheries Service). 2003. Resource survey report, bottom trawl survey, Cape Hatteras–Gulf of Maine: March 5, 2003–April 27, 2003, FRV *Delaware II*, 34 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[8] NMFS (National Marine Fisheries Service). 2003. Resource survey report: bottom trawl survey, Cape Hatteras–Gulf of Maine: September 7–November 1, 2003, FRV *Albatross IV*, 35 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, 02543.

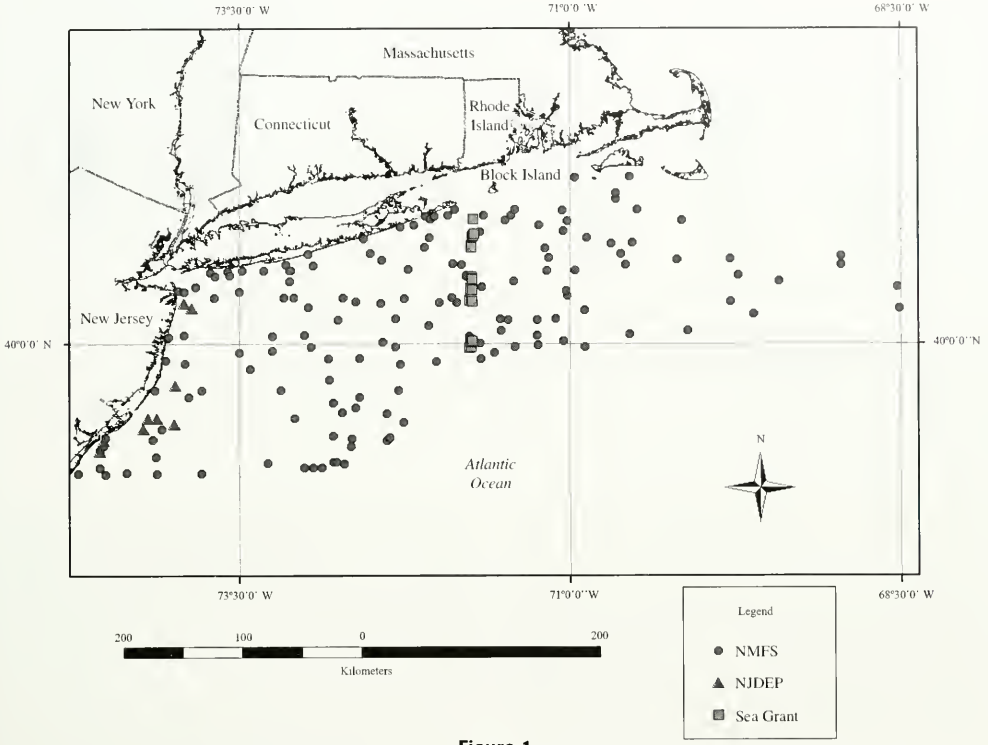

Figure 1

Map of fishery-independent sampling locations. Circles (●) are locations sampled during the National Marine Fisheries Service annual bottom-trawl survey cruise, triangles (▲) are locations sampled by the New Jersey Department of Environmental Protection, squares (■) are locations sampled during a Sea Grant sponsored cruise transecting the continental shelf along Block Island Sound Canyon.

To obtain an index of relative abundance, final mass values were divided by the number of tows made during each time of day, year, and seasonal period.

For Equations 1 and 2, values for P and R were estimated from longfin squid collected regionally during the winter, spring, and fall. Mantle lengths (mm) and the corresponding body weights (g) of individual squid measured in Hunsicker (2004) were used to calculate the percent distribution of biomass in each of the two size classes during each seasonal period. These estimated proportions were then used to partition the total catches reported at each NMFS station into prerecruit and recruit biomass. For each seasonal and diurnal period, catches were averaged between years and used to contrast relative concentrations of longfin squid in the demersal environment. Gear biases may affect the catchability of prerecruits more than recruits; therefore relative catch rates were compared among seasons only within each size class.

Sampling

Bluefish, goosefish, silver hake, and summer flounder were collected from continental shelf waters off the coasts of New York, New Jersey, Connecticut, Rhode Island, and Massachusetts from February 2002 to July 2003. Samples were obtained from two main sources: from fish landed by commercial fishing boats and from scientific survey cruises. Fishery-independent collections were made in conjunction with bottom trawl surveys conducted bimonthly by the New Jersey Department of Environmental Protection (NJDEP) and seasonally (except summer) by the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) (Fig. 1). Samples were also collected aboard the RV *SeaWolf* (Sea Grant) during an independent survey that transected the continental shelf along the Block Island Sound Canyon (Fig. 1). The proportion of samples collected from fishery-independent sources is shown in

Figure 2 and the number of samples collected from all sources during all seasons is shown in Figure 3.

In addition to the stomach contents collected and analyzed for the present study, diet data collected regionally were drawn from the NMFS-NEFSC bottom trawl survey database. A full description of the survey design and collection methods used by the NEFSC can be found in Azarovitz et al.[9]

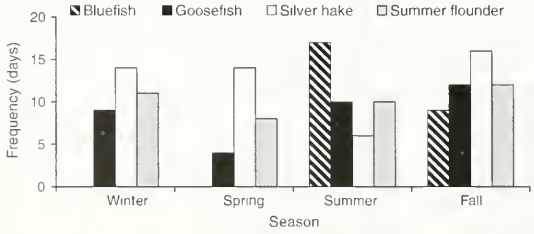

Figure 3

Frequencies (in days) of samples of bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americonus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) collected from fishery-dependent and fishery-independent sources. No samples were collected for bluefish (*Pomatomus saltatrix*) during the winter and spring seasons.

Diet analysis

The majority of samples obtained from fishery-independent sources were processed onboard research vessels. However, only cursory assessments of prey type and mass could be made at sea; therefore samples were frozen and transported to the laboratory for a more thorough examination. Each fish was weighed and measured (fork length for bluefish, total length for goosefish, silver hake, and summer flounder), stomachs were removed, prey items were weighed to the nearest 0.01 gram and identified to the level of species whenever possible. With the aid of a dissecting microscope, otoliths, beaks, and other hard parts were recovered in order to classify species. When stomach contents could not be identified because of advanced stages of digestion, they were recorded as "unidentified animal remains." As with all diet studies, there is always a chance that a portion of samples are biased because fish may feed while in the net. This problem was addressed by excluding fish where prey was found (undigested) in the mouth and esophagus or where there was a clear difference in digestion stage among prey items found in the stomachs.

Three size classes, covering the total range of lengths of fish collected, were chosen for each species as follows: bluefish—small (200 to 450 mm fork length), medium (451 to 550 mm), and large (>551 mm); goosefish—small (50 to 250 mm total length), medium (251 to 450 mm), and large (>451 mm); silver hake—small (50 to 199 mm total length), medium (200 to 299 mm), and large (>300 mm); and summer flounder—small (250 to 399 mm total length), medium (400 to 549 mm), and large (>550 mm). Seasonal time periods were defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

[9] Azarovitz, T., S. Clark, L. Despres, and C. Byrne. 1997. The Northeast Fisheries Science Center bottom trawl survey program, 22 p. ICES Council Meeting 1997/Y:33.

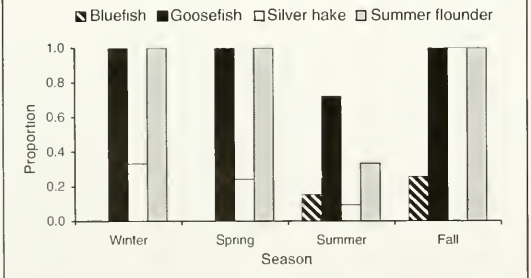

Figure 2

The proportion of samples of bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) specimens collected from fishery-independent sources. No samples were collected for bluefish during the winter and spring seasons.

Statistical analyses

The Kruskal-Wallis test was used to test seasonal and size-based differences in predation on squid. A nonparametric test was chosen because of its robustness to assumptions of normality and skewness (Quinn and Keough, 2003). Preliminary analyses indicated that none of the data sets fitted the normal distribution and, owing to large numbers of zero values (representing the absence of squid in the diet), could not be transformed. Two sets of tests were performed on the data: first an "aggressive" set of tests were run by using individual fish as the sampling unit to give the maximum number of degrees of freedom; second, a "conservative" set of tests were run by using either stations (for data collected from fishery-independent sources) or cruises (for data collected from commercial fishery sources) as the sampling unit. The percent mass of squid in the diet of each fish (aggressive test) or pooled fish per station or cruise (conservative test) was determined and expressed as a propor-

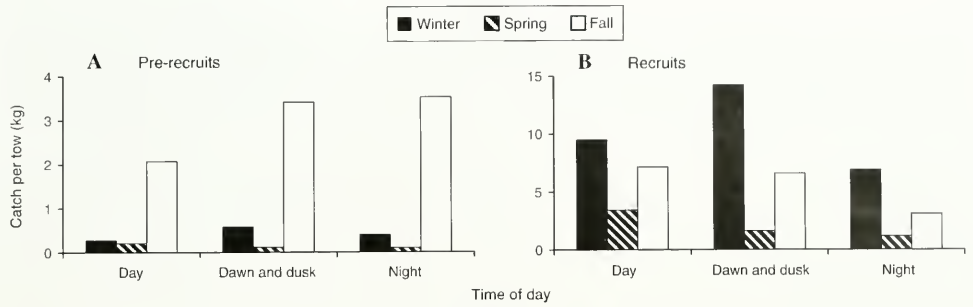

Figure 4

Relative catches of longfin inshore squid (*Loligo pealeii*) (**A**) prerecruits (≤80 mm mantle length) and (**B**) recruits (>80 mm mantle length) predicted in demersal waters during winter, spring, and fall of 2002 and 2003 (summer sampling was not conducted). Abundances of longfin inshore squid were measured as catch per tow (kg) and adjusted by seasonal diel correction coefficients specified in Hatfield and Cadrin (2002).

tion of the total mass consumed. To account for large numbers of tied rank values, an adjusted H test statistic was used to test the null hypothesis (Sokal and Rohlf, 1995). The two approaches produced similar results for the majority of tests. Therefore, only conservative test results are reported.

Results

Seasonal and diurnal differences in longfin inshore squid abundance

Predicted catches of longfin prerecruits during 2002 and 2003 indicated that the highest catch levels occured during the fall, intermediate levels during the winter, and minimum levels during the spring (Fig. 4A). These calculated values are similar to the historical abundance trends previously reported in Northwest Atlantic waters. Fall catches of prerecruits over all times of day were an order of magnitude higher in comparison to winter and spring values. The greatest variation in diurnal catches of prerecruits was predicted during the fall season (Fig. 4A). Conversely, catches of longfin recruits were estimated to be at their maximum during the winter, at intermediate levels during the fall, and at minimum levels during the spring (Fig. 4B). Maximum catch rates of longfin recruits were predicted during crepuscular and daytime periods of winter (Fig. 4B). Moreover, nighttime catches of recruits were two to three times higher during winter than during all other seasons.

Diet analysis

Bluefish Bluefish are present in Northern Atlantic waters only during the warmer months of the year; therefore sampling was restricted to the summer and fall seasons. A total of 299 bluefish from 26 sampling dates were analyzed. Fish ranged in size from 90 to 780 mm FL (average=469.6 mm). Overall, 53% of all bluefish sampled had food items present in their stomachs, and diets were split nearly equally between squid and fish. Perciforms were the dominant piscine prey; small amounts of amphipods and other pelagic crustaceans made up the remainder of the diet. A complete list of prey species recovered from all predator diets and their designated taxonomic groups can be found in Staudinger (2004).

Longfin squid was the primary squid species consumed by bluefish. A substantial amount of shortfin squid was also found in the stomachs of large fish (Table 1). Total predation on squid was greater during the summer than in the fall (Table 2); however, seasonal differences were not statistically significant possibly because of the high frequency of zero values in the dataset ($H_{adjusted}$=2.40, P=0.121, n=25). Medium and large fish were the primary consumers of squid, and small bluefish fed almost exclusively on fish (Table 1). Significant differences were found in the amount of squid consumed among all size classes of bluefish ($H_{adjusted}$= 6.62, P=0.037, n=75).

Goosefish A total of 536 goosefish stomachs were analyzed of which 269 (50%) contained prey. Goosefish ranged in size from 75 to 818 mm TL (average=341.1 mm). Goosefish were almost exclusively piscivorous; 93% of the total diet consisted of a mixture of gadiforms, clupeiforms, perciforms, and several other fish groups. Goosefish were the only species in the present study to prey on rajiforms.

Occurrence of squid in the goosefish diet was restricted to the winter and fall (Table 2) and differences among all seasons were significant ($H_{adjusted}$=15.27, P=0.002, n=46). Although medium size goosefish were

Table 1

Size-based stomach contents of fish collected in shelf waters of the Northwest Atlantic. Values presented are percentages of mass consumed (in grams). Fish lengths (small, medium, and large) are measured in millimeters. "Percent feeding" means the percentage of stomachs analyzed that contained prey. Bluefish were measured in fork length; goosefish, silverhake, and summer flounder were measured in total length.

	Bluefish			Goosefish		
Prey type	Small 200–450	Medium 451–550	Large 551+	Small 50–250	Medium 251–450	Large 451+
Squid	1.3	75.4	42.2	—	4.9	0.5
Longfin inshore squid	1.2	44.9	18.1	—	4.9	0.5
Northern shortfin squid	—	1.7	15.0	—	—	—
Unidentified squid	0.1	28.8	9.1	—	—	—
Fish	98.4	23.0	53.5	99.4	94.8	91.9
All other prey	0.3	1.6	4.3	0.56	0.24	7.68
Number of stomachs analyzed	103	99	113	148	153	235
Number containing prey (percent feeding)	76 (74)	51 (52)	49 (43)	96 (65)	75 (49)	98 (42)
Mean length (mm, SE)	316.6 (9.9)	509.8 (3.3)	628.6 (7.7)	124.8 (3.0)	358.2 (6.9)	540.0 (7.1)
Length range (mm)	200–438	460–547	555–780	75–241	255–450	460–818
	Silver hake			Summer flounder		
Prey type	Small 50–199	Medium 200–299	Large 300+	Small 250–399	Medium 400–549	Large 550+
Squid	0.0	2.7	18.6	16.7	33.5	20.6
Longfin inshore squid	0.0	2.7	12.3	15.3	25.4	14.7
Northern shortfin squid	—	—	0.2	—	—	5.3
Unidentified squid	—	0.1	6.1	1.4	8.1	0.6
Fish	34.7	17.6	62.0	67.2	55.1	76.0
All other prey	65.33	79.63	19.33	16.13	11.40	3.44
Number of stomachs analyzed	174	566	240	316	360	154
Number containing prey (percent feeding)	132 (76)	298 (53)	108 (45)	85 (27)	91 (25)	54 (35)
Mean length (mm, SE)	150.5 (3.1)	260.4 (1.5)	334.6 (3.9)	346.1 (4.4)	454.9 (4.1)	608.2 (6.4)
Length range (mm)	60–199	200–298	300–484	250–399	400–530	550–750

the only size class found to consume squid in notable amounts (Table 1), differences in the proportions of squid consumed among all size classes were not significant ($H_{adjusted}$=3.11, P=0.211, n=138). All squid found in the goosefish diet were classified as longfin squid.

Silver hake Of the 980 silver hake stomachs examined, over half (55%) contained prey. Silver hake ranged in size from 60 to 484 mm TL (average=248.3 mm). Feeding rates for silver hake were highest during the summer months and lowest during the spring and fall. Overall, silver hake fed primarily on fish and crustaceans, and lesser amounts of squid and other invertebrates. Amphipods and euphausiids were the dominant crustacean prey. Consumption of gadiforms, including conspecifics and unclassified osteichthyans, made up the majority of piscine prey.

Predation on squid differed significantly among seasons ($H_{adjusted}$=10.03, P=0.018, n=55) and was at its maximum during winter (Table 2). Silver hake diets exhibited a pronounced shift towards squid with increasing size (Table 1). Small and medium hake ate negligible amounts of squid. Conversely, squid totaled nearly 20% of all mass consumed by large hake. Differences in squid predation among size classes were significant ($H_{adjusted}$=7.58, P=0.023, n=132). Longfin squid was the dominant species of squid identified in the silver hake diet.

Summer flounder Of the 830 summer flounder analyzed, only 28% were found to be actively feeding. Summer flounder spend the juvenile stage of their life cycle in estuaries along the Northwest Atlantic coast; hence few flounder <280 mm were present in the analysis. Fish ranged in size from 250 to 750 mm TL (average=450.7 mm). Overall, diets consisted primarily of fish, squid, and stomatopods. Perciforms and clupeiforms were the dominant piscine prey.

Table 2

Seasonal stomach contents of fish collected in shelf waters of the Northwest Atlantic. Values presented are percentages of mass consumed (in grams). Fish lengths are measured in millimeters. No bluefish (*Pomatomus saltatrix*) were collected during the winter and spring seasons. "Percent feeding" means the percentage of stomachs analyzed that contained prey. Bluefish were measured in fork length; goosefish, silver hake, and summer flounder were measured in total length.

	Bluefish				Goosefish			
Prey type	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Squid	—	—	58.2	10.7	2.9	—	—	3.9
Longfin inshore squid	—	—	31.7	3.2	2.9	—	—	3.9
Northern shortfin squid	—	—	7.2	7.5				
Unidentified squid	—	—	19.3	—				
Fish	—	—	38.7	88.6	83.7	100.0	96.5	96.0
All other prey	—	—	3.1	0.7	13.39	0.00	3.45	0.13
Number of stomachs analyzed	—	—	236	67	206	22	259	49
Number containing prey (percent feeding)	—	—	114 (48)	45 (67)	58 (28)	8 (36)	175 (68)	28 (57)
Mean length (mm, SE)	—	—	495.0 (12.4)	405.9 (24.6)	462.1 (16.3)	523.8 (26.2)	273.4 (13.4)	462.1 (25.4)
Length range (mm)	—	—	230–737	90–780	160–780	420–620	75–818	170–690

	Silver hake				Summer flounder			
Prey type	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Squid	15.6	1.6	0.0	0.7	49.0	0.5	22.1	12.4
Longfin inshore squid	11.4	0.3	0.0	0.6	41.2	0.5	5.2	8.6
Northern shortfin squid	—	0.4	0.0	—	7.6	—	—	—
Unidentified squid	4.1	1.0	—	0.1	0.2	—	16.9	3.9
Fish	30.3	35.7	34.6	65.4	49.6	99.5	37.9	81.8
All other prey	54.1	62.7	65.3	33.8	1.40	0.04	39.93	5.76
Number of stomachs analyzed	308	365	165	143	407	103	120	196
Number containing prey (percent feeding)	163 (53)	165 (45)	146 (88)	64 (45)	77 (19)	22 (21)	65 (54)	66 (34)
Mean length (mm, SE)	270.7 (4.7)	262.8 (5.7)	198.5 (4.8)	268.0 (6.9)	477.5 (12.6)	446.9 (30.1)	431.2 (11.1)	439.7 (12.9)
Length range (mm)	60–484	79–480	103–410	110–450	270–710	300–750	268–645	250–690

The proportion of squid consumed by summer flounder fluctuated significantly among seasons ($H_{adjusted}$=14.29, P=0.003, n=43). Predation on squid was at its maximum during winter, and elevated during the summer in comparison to spring and fall (Table 2). Although differences in squid predation among size classes were not significant ($H_{adjusted}$=2.33, P=0.312, n=132), squid contributed the greatest relative amount to the diet of medium flounder (Table 1). The dominant species of squid identified in all size classes and for all seasons was longfin squid. Shortfin squid was found only in the diets of large flounder (Table 1) and only during the winter season (Table 2).

Discussion

Seasonal predation on squid

Previous descriptions of predation on squid in the Northwest Atlantic have been based on sampling in the fall and, to a lesser extent, during the spring seasons. Survey

cruises conducted by the NMFS during these two periods were the primary data source for these prior analyses. The present study indicates that these two seasons are not wholly representative of total predation pressure on squid; indeed, winter and summer may be primary periods for predation on squid. Consequently, previous estimates of the total predatory demand imposed on squid populations by these predators may have been underestimated (Buckel et al., 1999b; Overholtz et al., 2000). It should be noted that in order to collect adequate numbers of fish during all four seasons, fishery-dependent sources were used. However, nonrandom sampling could have influenced seasonal differences seen in the present study.

It is likely that heightened predation on squid during the winter season reflects an increase in habitat overlap by both predator and prey. All species of squid and fish evaluated in this study are known to retreat to warmer waters of the outer shelf and slope during the colder months of the year. This movement may act to concentrate fish and squid and lead to elevated predator-prey encounter rates. Predicted nighttime and crepuscular catches during winter indicate that longfin squid are at higher concentrations in the demersal environment than at other seasons and reflect diminished vertical migrations by squid (Hatfield and Cadrin, 2002). Increased residence time in bottom waters may make squid more susceptible to demersal predators and may explain their marked increase in silver hake and summer flounder diets during winter. Although the present study has made contributions to increase knowledge of predation rates during summer, data on squid abundance levels were insufficient to make inferences about predator interactions during this season.

Historically, longfin squid seasonal biomass on the shelf has been estimated to be at its maximum during the fall (Cargneli et al., 1999). This trend was reflected in catch results for prerecruits during the time period evaluated; however, this supposed increase in availability was not reflected in predator diets. Instead, summer flounder and bluefish both exhibited diminishing reliance on squid and increased predation on similar piscine prey (Staudinger, 2004). It is unclear whether predator and squid size relationships or predator preference is mediating bluefish and summer flounder foraging behavior; therefore further studies are warranted. Alternatively, it has been acknowledged that the NMFS fall bottom-trawl survey has better coverage of the shelf than the winter and spring surveys, as well as the greatest overlap with the distribution range of longfin squid.[10] Both of these factors could influence seasonal historical abundance estimates and inaccurately represent the fall population in relation to other times of year.

Size-based shifts in predation by fish

Ontogenetic shifts in feeding commonly take place in the early life stages of a fish. However, for many species, less is known about progressive shifts through the adult stages of growth (Gerking, 1994). Bluefish showed a dramatic shift in diet at lengths of approximately 450 mm, transitioning from a diet primarily of piscine prey to that of squid. Longfin squid was the dominant cephalopod identified in the diets across all sizes of bluefish; however, shortfin squid was found to increase in importance in large bluefish. It is at this larger (551+ mm) size that bluefish begin to inhabit outer-shelf and offshore waters (Fahay et al., 1999). Because shortfin squid are more pelagic than longfin squid (Brodziak and Hendrickson, 1999), this change in diet may reflect an ontogenetic shift towards offshore food resources as bluefish mature.

Silver hake also exhibited a strong and positive increase in predation on squid with increasing size. Significant differences were observed among size classes—the greatest amount of squid being consumed by fish 300 mm and greater. The size at which silver hake were found to begin feeding on squid is similar to that found in previous studies (Garrison and Link, 2000). However, the relative proportions consumed by large hake were found to be nearly double those previously reported. It is possible that the findings of the present study represent an expanded view of the silver hake diet at larger body sizes because of intensified sampling over all seasonal periods. Alternatively, increased squid consumption could reflect decadal differences in squid availability.

Summer flounder spend the juvenile stage of their lives in bays and estuaries. Link et al. (2002) reported squid in the diets of individuals smaller than those examined in the present study. Therefore, the initial shift toward squid by young flounder as they transition from inshore to offshore waters may not have been realized. In fish that were sampled on the continental shelf, squid were found to be an important constituent of diets across all body sizes. Although a statistically significant shift among size classes was not detected, predation on squid was observed to peak in medium-size fish. This finding is similar to that of Bowman et al. (2000), who determined squid consumption peaked between 500 and 600 mm and then declined again for larger fish.

Bowman et al. (2000) reported cephalopods as a major constituent (>20%) of the goosefish diet in the southern New England region. In a study conducted by Armstrong et al. (1996), longfin squid were found in small goosefish (<400 mm TL) stomachs during summer and represented approximately 10% of the diet. In contrast, the present study found that squid contributed trivial amounts to the diet of goosefish across all size classes and seasons. It is unclear why such vast discrepancies were observed between these studies. One possible ex-

[10] NEFSC (Northeast Fisheries Science Center). 2002. Report of the 34th northeast regional stock assessment workshop (34th SAW): stock assessment review committee (SARC) consensus summary of assessments. Northeast Fish. Sci. Cent. Ref. Doc. 02-06, 356 p. National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543.

planation is that the opportunistic foraging strategy of goosefish is more sensitive to variation in relative and overall abundances of prey and results in erratic food habits over various time scales.

Predator–prey behavior

Differences in the amount of squid consumed among species, among predator sizes, and seasonal periods indicate that aspects of predator and prey behavior must be playing a pivotal role in influencing the susceptibility of squid to predation. Seasonal inshore-offshore habitat use and diurnal vertical migrations are two mechanisms that may act to mediate predator-prey encounter rates. Other behaviors that influence encounter rates are the times of day that each predator is actively hunting and the areas of the water column being searched. Of the four predators evaluated, seasonal movements by summer flounder are most similar to the migration patterns of longfin squid. Summer flounder are primarily daytime feeders and spend the majority of their time on or near the seafloor (Packer et al., 1999). Conversely, silver hake are a demersal species known to be active hunters primarily in the late afternoon and evening (Bowman, 1984). Large vertical movements in the water column are not customary for silver hake (Bigelow and Schroeder, 1953), therefore nighttime feeding limits interactions during seasons when squid exhibit strong diurnal migrations. Bluefish are the only predator in this study considered to be pelagic and that actively pursue prey throughout the water column. Although bluefish have been shown to forage primarily during the day (Juanes and Conover, 1994), it is possible that there is a seasonal shift in depth at which bluefish forage (Bigelow and Schroeder, 1953). A shift from feeding at depth in the late spring and summer to feeding in the surface waters during fall may explain, in part, seasonal differences in importance of squid to bluefish because few (if any) squid are present in the upper water column during daylight.

In general, daytime foraging behavior, combined with positioning in the demersal environment, create the optimal setting for regular encounters between squid and fish predators and explain differences in the proportion or even presence of squid in the diet between species with similar geographical ranges.

Implications for management

Since the late 1980s, squid harvests have increased substantially during the winter. Offshore harvests have been, on average, three times greater than inshore catches between October and March (Cadrin[11]). The combination of increased fishing pressure and elevated predation rates concentrated within a single season may not be sustainable for a species, such as squid, with a life span of less than a year and that has little overlap between generations (Pierce and Guerra, 1994). If not properly accounted for, this increase in total mortality on squid during the winter could affect the number of squid surviving to spawn during spring and summer and limit available biomass for predators such as bluefish and summer flounder.

Another area of concern stems from potential increases in top-down pressure from recovering predator populations. Regionally, management has emphasized age-truncation of predators as one of the most serious factors affecting summer flounder and silver hake populations. The age classes of summer flounder (age-2) (Terceiro[12]) and silver hake (age-3) (Brodziak[13]) targeted for expansion in their respective management plans, correspond to the lengths and associated ages identified in the present study as being the most voracious predators of squid. If management objectives are met and summer flounder and silver hake stocks are fully rebuilt, predation on squid could rise substantially as fish that have been functionally absent from the population begin increasing in abundance.

Other species, such as bluefish, that have been severely overfished are also showing signs of recovery (ASMFC[14]). Consumption of squid by bluefish has been estimated to exceed the mass removed by the fishing industry (Buckel et al., 1999b) and is contingent on predator population abundance (Overholtz et al., 2000). If one includes summer foraging habits, total consumption of longfin squid by bluefish may be much greater than previously estimated. In light of this new information, a reassessment of the predatory demand imposed by bluefish and other recovering predators on squid is clearly needed before fish stocks are fully rebuilt.

The simultaneous exploitation of predators and their prey, when there is limited information about species interactions, is a precarious practice that can have unintended and potentially detrimental consequences for one or both stocks. Depletion of biomass that supports higher predators may decrease biological production. Conversely, prey populations may become overextended. A greater understanding of species relationships is necessary, especially in ecosystems where fishing occurs at multiple trophic levels. The present study shows that consideration of predation year-round and for a range of predator sizes is imperative to accurately assess

[11] Cadrin, S. X. 2001. Status of fishery resources off the northeastern United States: longfin inshore squid. Website: http://www.nefsc.noaa.gov/sos/spsyn/iv/lfsquid/ [accessed on 8 March 2006].

[12] Terceiro, M. 2003. Stock assessment of summer flounder for 2003. Northeast Fisheries Science Center Reference Document, 179 p. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, 02543.

[13] Brodziak, J. 2001. Status of fishery resources off the northeastern United States: silver hake. Website: http://www.nefsc.noaa.gov/sos/spsyn/pg/silverhake/ [accessed on 8 March 2006].

[14] (ASMFC) Atlantic States Marine Fisheries Commission. 2003. Website: http://www.asmfc.org [accessed on 8 March 2006].

predation pressure on squid populations. As predator populations in the Northwest Atlantic are recovered under current management initiatives, a multispecies management approach will be crucial to avoid conflicts between squid and finfish fisheries and should be applied to species beyond those presented in this article.

Acknowledgments

I thank T. Essington, R. Armstrong, F. Juanes, R. Cerrato, D. Conover, and four anonymous reviewers for their help with previous drafts of this manuscript; W. Kramer for querying data from the NMFS database; J. Palmer and L. Hendrickson for graciously providing stock assessment information; and Inlet Seafoods, Alice's Seafood, and Soleau's Wharf and Marina for providing fish for diet analyses. This research was funded by the New York Sea Grant Institute. Work was conducted at the Marine Science Research Center at Stony Brook University as part of a Master of Science thesis.

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Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington

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Resource partitioning among co-occurring species can provide evidence that density-dependent survival can be a function of interspecific competition. Of the early life history stages of flatfish, the juvenile phase is thought to be the most susceptible to density-dependent mortality, and intraspecific competition among individuals is thought to lead to decreased survival of extremely strong year classes (Iles and Beverton, 2000). Juveniles of multiple flatfish species are often observed to coexist in a single nursery area (e.g., Burke et al., 1991; Henderson and Holmes, 1991; Reichert and van der Veer, 1991; Norcross et al., 1997), but evidence for interspecific competition is rarely examined. We examined evidence for resource partitioning and interspecific competition among juvenile flatfish species co-occurring in nursery areas.

Flatfish species often have juvenile nursery areas that are segregated from the adult population. In many cases, juveniles use shallow nearshore habitats as nursery areas, and adults are found in deeper offshore habitats (Gibson, 1994; van der Veer et al., 2000). On the Pacific coast of North America, estuaries are typically smaller and occur less frequently than in other areas such as the Atlantic coast of North America. Possibly because of the limited estuarine habitat on the West Coast, fewer species of marine fish and invertebrates use coastal estuaries for nursery areas. In our study, we examined the spatial distribution of co-occurring juvenile flatfish populations within Pacific coast estuaries. The four species examined were English sole (*Pleuronectes vetulus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), and starry flounder (*Platichthys stellatus*). Juveniles of these species are found in Oregon and Washington estuaries during the summer, and adults of each of these species contribute to a lucrative trawl fishery on the coastal shelf.

To date, estuarine residency of juvenile English sole has been well documented (Krygier and Pearcy, 1986; Gunderson et al., 1990; Rooper et al., 2003); however, this is the first comparison of the spatial distribution of the three other species within estuaries, and is the first study to encompass such a wide region of coastal estuaries (ranging over 400 km of coastline). The goal of this study was to compare the summer distribution of juvenile English sole, starry flounder, sand sole, and Pacific sanddab within nursery estuaries over three years, to determine whether the four flatfish species were spatially partitioning the nurseries. We also examined the summer distribution in relation to the abundance of species across years and habitats in order to determine the potential for interspecific competition.

Materials and methods

Study area

This study was carried out at four estuaries on the Oregon and Washington coasts: Grays Harbor, Willapa Bay, Coos Bay, and Yaquina Bay (Fig. 1). Seventeen to 20 trawl sites were chosen within each estuary, and each trawl site was classified into three habitat types: lower main channel, lower side channel and upper estuary. Habitat delineations were previously identified by principle component and discriminant function analysis (Rooper et al., 2003). The lower estuarine sites were on average deeper (depth=5.1 m), colder (13.6°C), and more saline (28.5 ppt) than upper estuarine sites because of their proximity to the mouth of the estuary. On average, lower side channel sites were slightly warmer (15.6°C), shallower (depth=3.7 m) than the lower estuarine sites, and had extensive tide flats that surrounded the sites and were exposed during low tides. Upper estuarine sites were typically shallow (depth=4.0 m), very warm (17.0°C), less saline (25.1 ppt), and had a large sediment size and a smaller area of surrounding tidal flats (Rooper et al., 2003).

Sampling procedures

Trawl surveys of all four estuaries were conducted in both June and August from 1998 through 2000. In each month all four estuaries were sampled over two and a half weeks and a total of 431 trawl hauls were completed over the three summers. The same sites were resurveyed throughout all years of sampling; however the exact trawl location varied somewhat between sampling

Manuscript submitted 8 September 2004 to the Scientific Editor's Office.
Manuscript approved for publication 3 November 2005 by the Scientific Editor.
Fish. Bull. 104:616–622 (2006).

Figure 1

Map of coastal Oregon and Washington with insets showing the four estuaries studied: Grays Harbor (total subtidal area=8545 ha), Willapa Bay (total subtidal area=11,200 ha), Yaquina Bay (total subtidal area=471 ha), and Coos Bay (total subtidal area=1195 ha).

periods by approximately 50 m. Benthic organisms, including the four target flatfish species, were collected during daylight with a beam trawl (Gunderson and Ellis, 1986). The beam trawl had an effective opening width of 2.3 m and a height of 0.6 m. The net was towed at a speed of 0.8–0.9 m/s behind a 6.4-m research vessel with a minimum 5:1 scope of line out to depth. The distance towed averaged 139 m in 1998–2000. Trawls were made against the prevailing current over a variety of tide stages, although efforts were made to conduct trawling near the time of daylight slack low water. Sampling was not conducted at high current velocities during maximum ebb and flood tides to ensure the greatest adherence of the beam trawl to the substratum. All fish and invertebrates captured were identified to species and English sole were measured for total length (TL) to the closest 1.0 mm. Other species of flatfish were measured (TL) only in 1999 and 2000.

Data analysis

There was considerable variability in the data associated with each sampling period that was not related to habitat use. This variability was due to other factors, such as patterns in interannual variability in recruitment to individual estuaries or to differences in overall abundance among the four flatfish species. To minimize the effect of this variability on the analyses, it was

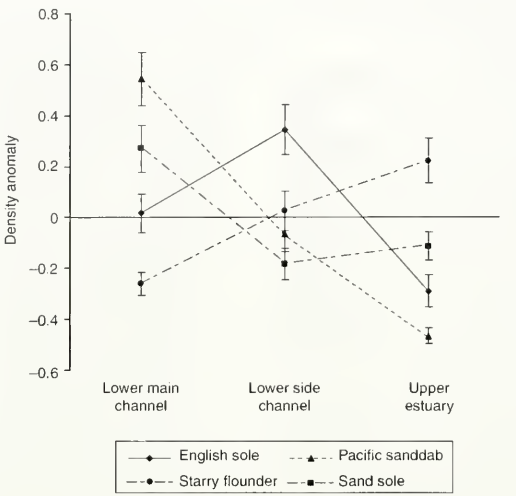

Figure 2

Average density anomaly (and standard error bars) for English sole (*Pleuronectes vetulus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), and starry flounder (*Platichthys stellatus*) by habitat type across all study estuaries, months, and years.

necessary to standardize the data within each estuary. We used the normalized anomaly (Zar, 1974) of flatfish densities as the dependent variable to compare use of habitats within estuaries for each species, where

$$a_i = \frac{x_i - \bar{x}_{emy}}{sd_{emy}} .$$

In this equation the subscript i refers to an individual density from a trawl survey site within an estuary-month-year combination, *emy* refers to the estuary-month-year combination where a trawl survey occurred, and $\bar{x}$ and sd are the mean and standard deviation of all trawl surveys occurring in that estuary-month-year combination. By using the anomaly of the densities, we reduced the variation in the data that was attributed to estuarine, seasonal, and interannual sources in order to concentrate solely on the within-estuary component of variation. For example, if the average catch of Pacific sanddab was 1000/ha for the Grays Harbor estuary in June 2000, individual trawl hauls from Grays Harbor in June 2000 with catches <1000/ha would have a negative density anomaly, whereas trawl hauls with Pacific sanddab catches >1000/ha would have a positive density anomaly.

The density anomalies were analyzed by using analysis of variance (Zar, 1974). The full model used to analyze spatial distributions of each species included the main effects of habitat type, month of survey, year of survey, and estuary, as well as estuary-habitat, month-habitat, and year-habitat interaction terms. The interaction terms were specifically included to test the hypotheses that spatial distribution of each flatfish species was consistent across estuaries, years, and months. All significant ($P<0.05$) main effects and interactions were compared for significant differences among effect levels by using the least squares mean approach as a *post hoc* test with a Tukey's adjustment for multiple comparisons (Zar, 1974).

Results

Juvenile Pacific sanddab collected during the trawl surveys ranged in length from 23 to 150 mm TL. The analysis of Pacific sanddab density anomalies for habitat types within estuaries resulted in significant differences among habitats in the estuaries. There were significantly higher density anomalies in lower main channel habitats and significantly lower anomalies in upper estuary sites (Fig. 2). Lower side channels usually had

negative density anomalies—the most notable exceptions being Willapa Bay and Grays Harbor in 1998 (Fig. 3). This pattern produced significant interactions between habitat and both year and estuary.

The lengths of sand sole captured by trawling were comparable to those for Pacific sanddab, ranging from 20 to 234 mm TL, and only 12 specimens longer than 150 mm TL. Sand sole catch was highly variable across all systems, and there were 318 zero catches over the total 431 trawls. Sand sole density anomalies followed a pattern similar to those of Pacific sanddab. Density anomalies were significantly higher at lower main channel sites than at other sites within the estuary (Fig. 2). Density anomalies were similar between upper estuary sites and lower side channel sites. There were no significant interaction terms between estuary or year and habitat type; thus the pattern in spatial distribution of sand sole appeared to be consistent across estuaries and years.

Starry flounder were the least common species of flatfish captured in the study estuaries. The starry flounder captured were larger than the other species of flatfish, ranging from 49 to 376 mm TL, and 44 individuals were >150 mm TL. Density anomalies were highest at upper main channel sites (Fig. 2). As with sand sole, there were no significant interaction terms between habitat type and either estuary or year. The effect of habitat type on starry flounder densities was thus a consistent effect observed across all estuaries and years.

English sole lengths ranged from 14 to 200 mm TL and only 12 individuals were greater than 150 mm TL. English sole density anomalies were significantly higher at lower side channel sites than at other estuarine locations (Fig. 2). There was also a significant interaction term between habitat type and month. In August there was no significant difference between density anomalies in lower side channel and lower main channel sites, while in June density anomalies were much larger in lower side channels than at all other locations. The significant month and habitat type interaction in the analysis of English sole density anomalies was most likely due to habitat changes observed in juvenile English sole as they grow (Rooper et al., 2003). A carrying capacity for large (>50 mm TL) English sole was observed in the study estuaries, and large English sole distribution expanded when densities were high (Rooper et al., 2003). The expansion of English sole distribution when densities were large corresponds to an increase in the density anomalies of Pacific sanddab in lower main channel areas (Fig. 4). Conversely, as large (> 50-mm-TL) English sole densities decreased, Pacific sanddab appeared to increase their distribution in the estuaries, as observed in higher density anomalies in lower side channels.

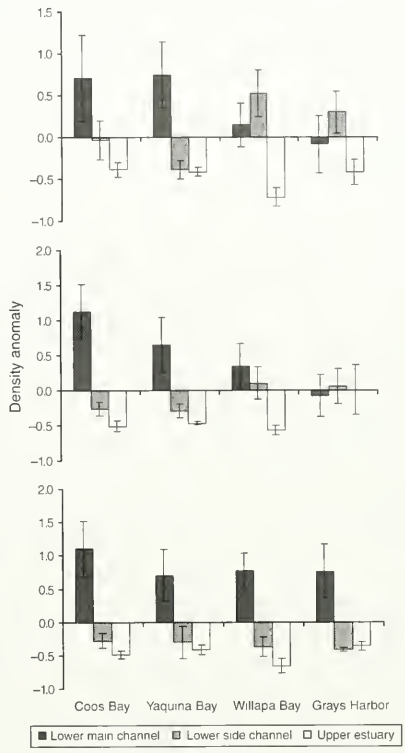

Figure 3

Pacific sanddab (*Citharichthys sordidus*) density anomalies (and standard error bars) by estuary and habitat type from 1998 (upper panel) through 2000 (lower panel).

Discussion

We observed evidence for resource portioning in four species of co-occurring juvenile flatfish in west coast nursery estuaries. The analysis of density anomalies indicated that the four flatfish species exploit different areas of estuaries. The spatial segregation among juvenile flatfish species observed in our study is consistent with results of other studies and indicates the potential for interspecific competition among the four species. Surveys of flatfish assemblages in Puget Sound, Washington have revealed spatial segregation of juvenile flatfish by depth, although the pattern was not consistent among sites (Thornburgh, 1980). In Thornburgh's study, spatial segregation may have been driven by differences in sediment type at the sites and by differences in settling times among the dominant species: English sole, sand sole, Pacific sanddab, and rock sole (*Lepidopsetta bilineata*). Distinct patterns in spatial distribution have also been observed for juvenile flatfish assemblages beyond the Pacific Northwest. In estuaries along the California

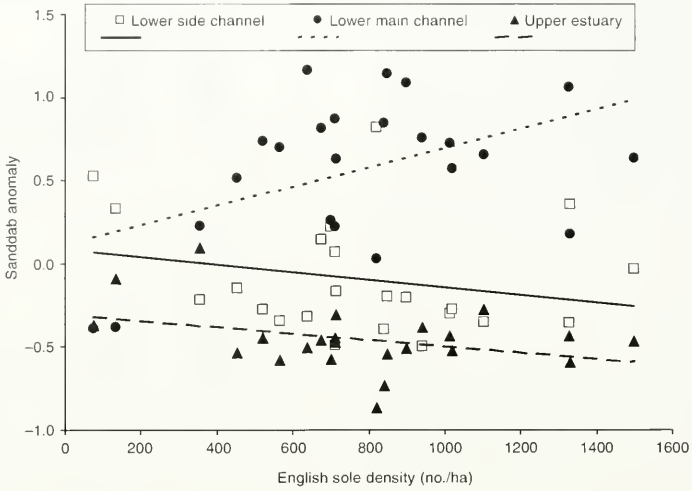

Figure 4

Average Pacific sanddab (*Citharichthys sordidus*) density anomaly compared to density of English sole (*Pleuronectes vetulus*) >50 mm TL at each location in the study from 1998 through 2000.

Bight, diamond turbot (*Hypsopsetta guttulata*) settle in the upper portions of bays during January and March, whereas California halibut (*Paralichthys californicus*) are found closer to bay entrances and the open coast, settling from March to September (Kramer, 1991). Settlement timing has also been found to be an important partitioning factor for common dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) in a small Scottish bay, where plaice settle earlier in the year than dab (Steele and Edwards, 1970). Depth has been identified as an important factor in partitioning nursery areas for the common dab and age-0 plaice (Edwards and Steele, 1968; Gibson, 1973). Juvenile flatfish in Alaskan inlets have also been found to segregate with depth and a number of other factors, such as temperature and sediment type (Norcross et al., 1997). Habitat type has also been found important in determining the spatial segregation of northeast Atlantic flatfish assemblages; ontogenetic shifts in habitat use occur in some species (Walsh et al., 1999; Phelan et al., 2001).

These studies indicate that flatfish species that exist together in nursery areas can partition resources in a number of ways according to biological (i.e., diet) or physical (i.e., depth or salinity) requirements, or according to a combination of both biological and physical requirements. Studies of shallow water habitats have generally indicated that flatfish in nursery areas are not limited by food resources (Evans, 1983). In west coast estuaries food resources can be quite high, especially in intertidal areas (Gunderson et al., 1990; Dumbauld et al., 2000). After review of diet studies documenting feeding differences among Pacific sanddab and English sole (Hogue and Carey, 1982; Thornburgh, 1980), as well as the abundance of food within the nursery area, we do believe it is unlikely that direct competition for food is solely responsible for the apparent pattern in estuarine distributions between the two species. We suggest that the segregation observed in northwest estuaries is most likely caused by differences in physical conditions of the habitat.

The four species of flatfish observed in the present study probably partition the nursery estuaries along gradients of salinity and temperature. Starry flounder were found in upper reaches of the estuary to a greater degree than the other species—a finding that is consistent with their ability to tolerate low salinity (Orcutt, 1950). Starry flounder were most abundant in Yaquina Bay, where the coverage of trawl survey sites extended farther up the estuarine salinity gradient than in other estuaries. The average salinity in June was 16–18 ppt at the uppermost Yaquina Bay sites, whereas the average June salinity at sites in other estuaries was always greater than 19 ppt. Salinity has been found to be an important determinant of the distribution of other flatfish species (Coggan and Dando, 1988; Marchand, 1988; Kerstan, 1991; Gibson, 1994; Marshall and Elliot, 1998).

The temperature preferences of English sole may allow them to exploit areas of the estuary not used extensively by Pacific sanddab. Temperatures less than 17.5°C have been observed to lead to high English sole growth (Yoklavich, 1982). These temperatures were observed in lower side channels of the study estuaries. For the speckled sanddab (*Citharichthys stigmaeus*), a close relative of the Pacific sanddab, maximum growth has been observed from 8° to 13°C (Ehrlich et al., 1979). This temperature range is closer to the temperatures found in lower side channels, and lower than the temperature range found in lower main channels in our study area. Thus, the Pacific sanddab, if it has temperature tolerances similar to those of its congener, may be limited to lower main channel locations in order to optimize growth rates, whereas optimal English sole growth occurs at the higher temperatures found in lower side channels.

An alternative explanation for Pacific sanddab distribution may be found in its response to high English sole density. The changing distribution of Pacific sanddab, when confronted by high densities of English sole, provides evidence that competition may occur between these two species. When English sole densities are high, Pacific sanddab seem to be limited in distribution to lower main channel locations (sites not preferred by English sole), and when English sole densities are low, Pacific sanddab appear to be more evenly distributed throughout the estuary. This pattern does not apply to starry flounder or sand sole, whose distributions remain the same regardless of English sole density. The implication of this resource partitioning is that English sole year-class strength may be affecting the ability of Pacific sanddab to use areas of the estuaries where conditions are optimal for flatfish growth.

Distinct patterns of habitat use by juvenile English sole, starry flounder, sand sole, and Pacific sanddab were observed in all four estuaries that we examined. Highest densities of Pacific sanddab and sand sole were found in lower main channel sites, highest densities of English sole were found in lower side channels, and highest densities of starry flounder were found in upper estuarine sites. These patterns of spatial segregation were consistent from 1998 through 2000. The patterns were consistent across the four estuaries encompassing 400 km of coastline. Resource partitioning is probably based primarily on temperature and salinity tolerances and growth preferences of the individual flatfish species; however, there is evidence of competition between English sole and Pacific sanddab when their spatial distributions are examined in response to their relative abundances.

Acknowledgments

Assistance in the field provided by Tim Loher, Jennifer Boldt, Geoff Hosack, Grace Tsai, Noble Hendrix, Neil Banas and Kirsten Holsman was greatly appreciated. This research was funded by the National Oceanic and Atmospheric Administration's Coastal Ocean Program under award no. NA96OP0238 to the University of Washington.

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Length-specific brood size and winter parturition in pink seaperch (*Zalembius rosaceus*) (Perciformes: Embiotocidae)

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The viviparous pink seaperch (*Zalembius rosaceus*) is considered unusual among other embiotocids because of its deep-water habitat (Tarp, 1952), winter parturition (Goldberg and Ticknor, 1977), small brood size (Baltz, 1984), and apparent lack of a positive relationship between brood size and female size (Baltz, 1984). In the present study, I present further support that parturition in pink seaperch occurs in winter and new evidence indicating length-specific brood sizes in the species.

Pink seaperch are found in deep water (to 229 m: Miller and Lea, 1972) over soft bottom (Allen, 1982) year-round off the coasts of California and Baja California (Eschmeyer et al., 1983). Mating occurs in spring and parturition occurs in winter (Goldberg and Ticknor, 1977)—a unique breeding schedule among surfperches. Other surfperches mate in summer or fall and give birth the following spring or summer when food for offspring is plentiful. For reasons that remain unclear, brood size for pink seaperch is considered low (mean=3.5: Goldberg and Ticknor, 1977) compared to other small-size (<160 mm) surfperches (reviewed in Baltz, 1984).

A positive relationship between brood size and female size is generally the rule among fishes (Bagenal, 1978) and is observed in all surfperches with the exception of pink seaperch (Baltz, 1984). However, data for the species are dubious because near-term females tend to abort their young during the time of collection (Baltz and Knight, 1983; Baltz, 1984)—a behavior that can result in both underestimates in brood sizes and high variability in length-specific brood size.

The goal of this study was to evaluate characteristics of the reproductive biology of pink seaperch using samples taken during periods both early and late in the breeding season. I predicted that estimates in length-specific brood size for females collected later in the season should be significantly smaller than those collected earlier if, in fact, near-term females have a high probability of aborting embryos. Similarly, I expected to see higher variability in relationships between length-specific brood size and female size in the late, compared to early, period of the breeding season.

Materials and methods

Specimens of female pink seaperch were collected with a 7.6-m (headrope) otter trawl with 1.3-cm codend mesh on the Palos Verdes shelf near Point Fermin, CA (33°41′N, 118°19′W) in fall (September and October, at 54 and 60 m depth, respectively) 1994 and in winter (January, at 66 m depth) 1995. Females were distinguished from males by having either a rounded belly or by lacking a fleshy reproductive organ on the anterior portion of the anal fin (Tarp, 1952). Gravid females collected in winter were stored separately in sealable bags to ensure that any embryos subsequently born were included in brood size records; females collected in fall had no evidence of premature births nor were there any premature embryos present in fall collections (see Results section). Individuals were placed on ice, frozen, and processed within 10 days. Females were dissected and the following information was recorded: standard length (SL ±1 mm), body mass (±1 g), brood size, embryo SL (±1 mm), embryo mass (±0.01 g), and evidence of premature birthing. From the appearance of females that had evidently expelled their broods while in storage bags, I recorded a female as having prematurely given birth if her ovary was devoid of embryos, flaccid, and contained traces of fresh blood. The relationships between female and brood size for fall and winter were analyzed separately by using regression analyses (SPSS, vers. 10, SPSS, Inc., Chicago, IL). Females showing evidence of recent expulsion were not included in brood size analyses.

Results

The size distribution of females captured varied between seasons (Fig. 1). The mean standard length (SL) of females in fall and winter was 125 mm (±15 mm SD, n=27) and 96 mm (±21 mm SD, n=76), respectively, and this difference was significant (t-test: t=6.82, df=101, P<0.001). All females greater than or equal to 100 mm SL (n_{fall}=26, n_{winter}=31) were sexually mature, having either embryos or evidence of recent expulsion of embryos. Among the mature females, the mean SL in fall and winter was 127 mm (±14 mm SD, n=26) and 117 mm (±9 mm SD, n=31), respectively, and this difference was also significant (t-test: t=3.19, df=55, P=0.002).

Both mean brood size and the relationship between female size and brood size varied between seasons (Fig. 2A). Mean brood sizes in fall and winter were seven (±3 SD) and three (±1 SD), respectively, and this

Manuscript submitted 21 March 2005
to the Scientific Editor's Office.
Manuscript approved for publication
21 November 2005 by the Scientific Editor.
Fish. Bull. 104:623–625 (2006).

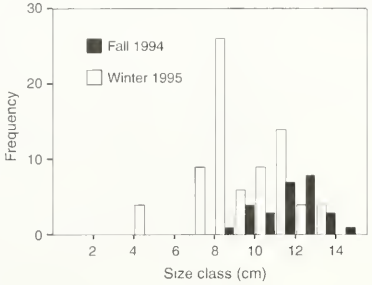

Figure 1

Size distribution for mature female pink seaperch (*Zalembius rosaceus*) (n=103) collected in fall 1994 (black bars) and winter 1995 (white bars). Bars represent 1-cm size classes.

difference was significant (t-test: t=5.15, df=55, P<0.001). The incidence of premature births for winter females was 18% (seven of 38 females) compared to 0% (0 of 27 females) for fall females, and differed significantly (Fisher's exact test: P=0.04). Female size was a good predictor of brood size in fall but not in winter (fall: r^2=0.39; winter: r^2=0.00, Fig. 2A).

Embryos were more developed and larger in winter than fall, and larger females brooded larger-sized embryos (Fig. 2B). Fall embryos had a mean SL of 21.3 mm (±4.2 mm SD) and were characterized by pale pink coloration, translucent tissue, and the absence of distinct scales. Winter embryos had a mean SL of 36.4 mm (±5.8 mm SD) and had firm and opaque tissue, distinct scales, iridescent pink coloration, and appeared as miniature adults. In both fall and winter, linear regressions of embryo-on-female size were significant (fall: r^2=0.17; winter: r^2=0.20, Fig. 2B).

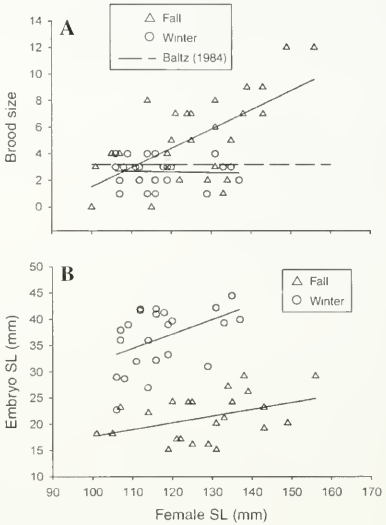

Figure 2

Linear regressions of (**A**) brood size (fall: r^2=0.39, brood size=−12.9 + 0.14x, n=26; winter: r^2= 0.00, n=31), and (**B**) embryo size (fall: r^2=0.17, embryo SL=4.9 + 0.13x; winter: r^2=0.20, embryo SL=4.2 + 0.28x) on female size for fall (triangles) and winter (circles) collections of pink seaperch (*Zalembius rosaceus*). Dashed line in A represents data from Baltz (1984).

Discussion

Both embryo characteristics and female reproductive condition provided evidence of winter parturition in pink seaperch and confirmed conclusions made by Goldberg and Ticknor (1977). Winter embryos had advanced morphological characteristics similar to those of adults, compared to embryos examined in fall, and were similar in size to those reported by Goldberg and Ticknor (1977). Evidence of a relatively high incidence of abortion and presence of many embryos (n=51) in winter collections provided further evidence that parturition occurs in or around January. Winter parturition is unique among surfperches yet no studies, to the author's knowledge, have provided an explanation for the unusual breeding schedule of pink seaperch.

Results from this study demonstrate a positive relationship between brood size and female size in pink seaperch, contrary to results of previous reports. Brood size increased with female size in fall but not in winter (Fig. 2A) in this study. The lack of a relationship observed in winter was similar to previous conclusions (See Fig. 2 in Baltz, 1984). Baltz and others (Goldberg and Ticknor, 1977; Baltz and Knight, 1983) speculated that sample effects may have explained the lack of a relationship between brood size and female body size, but no clear evidence was provided. In the present study, there was a high incidence of females (18%) that had aborted all embryos (i.e., complete abortion) among winter collections, and these females were excluded from analyses. However, partial abortions may occur in embiotocids (Schultz, 1993) presenting the possibility of underestimating brood size. Females with partially aborted broods were not identified nor excluded from the present study. Therefore, if such behavior occurred among large winter females, it would provide a reasonable explanation for the lack of relationship observed between brood size and female size.

Winter females had larger brood sizes than their fall counterparts and a higher frequency of abortion, providing evidence that winter females had partial rather than complete broods. Individuals smaller than the

mesh size of the net were present in winter collections, probably aborted by females stressed during capture. The number of embryos (n=51) present in the winter collections was higher than would be expected if they had been aborted by females having shown evidence of complete abortions (n=7). Therefore, pink seaperch have length-specific brood sizes as observed in other surfperches, and this finding is supported by the more reliable fall data from the present study.

Mean brood size for pink seaperch in the present study was higher than previously reported for the species. Goldberg and Ticknor (1977) reported that females had an average brood size of 3.5, which was similar to mean brood sizes obtained for winter collections in this study; however, according to arguments already presented, winter data likely resulted in an underestimation of brood size. Both mean and maximum fall brood sizes (max=10) were greater than winter brood sizes and greater than the brood size in samples examined in Goldberg and Ticknor's (1977) study. If brood size estimates in the Goldberg and Ticknor (1977) study included females collected in winter, the authors probably underestimated brood size, as well. The mean brood size of pink seaperch is similar to that of other deep water fishes (Koslow et al., 2000) but is considered relatively small compared to other embiotocids (reviewed in Baltz, 1984).

An unexpected result from the present study was evidence that large female pink seaperch have an earlier breeding schedule than small females. Reproductively active females in fall were larger on average than winter females (Fig. 1), indicating that large females left breeding sites earlier or that small females arrived at breeding sites later. Although greater temporal resolution of changes in size distribution would have been desirable, further evidence for size-dependent breeding was apparent from female- and embryo-size relations. In both fall and winter, embryos in large females were larger than embryos in small females (Fig. 2B), which would be expected if the reproductively active females in fall bred earlier than those in winter. An alternative explanation for the positive relationship between female size and embryo size would be that embryos in large females develop faster than those in small females because of greater maternal investment. I did not have sufficient data on embryo development because this was not the focus of my study; however, it is a hypothesis that warrants further investigation. Delayed breeding by smaller females of pink seaperch is a pattern observed in other surfperches (Eigenmann and Ulrey, 1894; Hubbs, 1921; Schultz, et al., 1991) and may arise from both energetic limitations on the time of reproduction and fitness advantages accrued by postponing reproduction and diverting additional energy towards growth (Schultz, et al., 1991).

Acknowledgments

Fish were collected in accordance with permits issued to California State University at Long Beach, Southern California Coastal Water Research Project, and the County Sanitation Districts of Los Angeles. This work was supported by the California State University at Long Beach (CSULB) and Southern California Coastal Water Research Project (SCCWRP). R. Flores, T. McSparren, and K. Mickey (all of CSULB) provided invaluable discussions and laboratory and field assistance. I am grateful to M. J. Allen (SCCWRP), J. Cross (SCCWRP), K. Mickey, E. T. Schultz, and two anonymous reviewers for comments and suggestions on earlier drafts of this manuscript.

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Aging fish otoliths recovered from Pacific harbor seal (*Phoca vitulina*) fecal samples

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Seals and sea lions are opportunistic predators that feed on a variety of fish and cephalopods, including some commercially and recreationally important species. Concerns over their interactions with commercial and sport fishing operations, and other human activities, has a long history in the Pacific Northwest (Everitt and Beach, 1982). The perceived increase in such interactions led, in part, to the U.S. Congress amending the Marine Mammal Protection Act (MMPA) in 1994. Chief among the amendments was a call for research to determine 1) whether California sea lions (*Zalophus californianus*) and Pacific harbor seals (*Phoca vitulina*) were affecting the recovery of listed or depleted salmonids, and 2) what broader impacts they may have on the coastal ecosystems of Oregon, Washington, and California (NMFS, 1997). In this note, we begin to address the latter question. Specifically, we describe a novel application of otolith aging techniques that can be used to increase the understanding of pinniped foraging ecology and, thus, their potential impact on the fishery resources of coastal ecosystems.

The Oregon Department of Fish and Wildlife's (ODFW) Marine Mammal Research Program has studied harbor seal foraging habits since the mid-1980s, primarily through the collection and analysis of scat (fecal) samples (Riemer and Brown, 1997; Riemer et al.[1]; Wright et al.[2]). Our results, as well as those from other pinniped food habit studies in Oregon (Graybill, 1981; Brown and Mate, 1983; Roffe and Mate, 1984; Orr et al., 2004), indicate that these animals consume a large number of diverse prey species. Concurrent research in Oregon indicates that Pacific harbor seals have increased significantly following protection under the MMPA; Brown et al. (2005) estimated that the 2002 statewide population total was 10,087 individuals. As noted above, these types of increases in pinniped abundance have led to more frequent interactions with coastal fish resources and hence an increased interest in the composition and abundance of prey in their diet.

Fortunately, new techniques have recently been developed to analyze pinniped diets. For example, rather than using traditional methods that rely strictly on otoliths (fish ear bones) for identifying prey, many researchers now try to identify all skeletal structures recovered from scats, which provide a more complete picture of pinniped diets (Olesiuk et al., 1990; Cottrell et al., 1996; Riemer and Brown, 1997; Browne et al., 2002). In addition, researchers are beginning to use molecular genetic methods to provide greater resolution in determining diet composition (Purcell et al., 2004; Deagle et al., 2005; Kvitrude et al., 2005). In this note, we add to this growing list of techniques by describing a novel use of fish otolith aging techniques to further our understanding of pinniped diets.

Fisheries scientists have aged fish otoliths to aid in the management of commercial and recreational fisheries (Love et al., 2002). Marine mammal scientists, on the other hand, have relied upon the identification of otoliths recovered from scats to identify the prey of pinnipeds (Brown and Mate, 1983; Beach et al.[3]; Harvey, 1989; Pierce and Boyle, 1991). However, the age of prey has rarely been considered when describing seal and sea lion diets. We believe that estimates

[1] Riemer, S. D., R. F. Brown, B. E. Wright, and M. Dhruv. 2001. Monitoring pinniped predation on salmonids at Alsea River and Rogue River, Oregon: 1997–1999. Unpubl. Contract Rep. to Pacific States Marine Fisheries Commission, NOAA Grant No. NA87FX0464, 38 p. [Available from OR Dept. Fish. and Wildl., 7118 NE Vandenberg Ave., Corvallis, OR 97330.]

[2] Wright, B. E., R. F. Brown, S. D. Riemer, and A. M. Ougzin. 2002. Pinniped predation on adult salmonids in the Alsea Estuary, Oregon. Unpubl.Contract Rep. to Pacific States Marine Fisheries Commission, NOAA Grant No. NA17FX1603, 35 p. [Available from OR Dept. Fish. and Wildl., 7118 NE Vandenberg Ave., Corvallis, OR 97330.]

[3] Beach, R. J., A. C. Geiger, S. J. Jeffries, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC (Northwest Alaska Fisheries Science Center) processed rep. 85-03, 316 p. NWAFC, National Marine Fisheries Service, Northwest Region, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.

Manuscript submitted 1 June 2005
to the Scientific Editor's Office.

Manuscript approved for publication
29 November 2005 by the Scientific Editor.

Fish. Bull. 104:626–630 (2006).

of the age of prey will result in a more comprehensive picture of pinniped diets and help to augment stock assessments that use age-specific models. We report our application of these techniques to Dover sole (*Microstomus pacificus*) otoliths recovered from Pacific harbor seal scat samples collected in an Oregon estuary. Dover sole were selected as a case study because they are a common prey of harbor seals in Oregon (Riemer and Brown, 1997) and their otoliths have been aged successfully in previous studies (Hagerman, 1952; Brodziak and Mikus, 2000).

Materials and methods

We conducted our study during the spring and summer of 1996, and year-round from 1997 through 2002, in the Alsea Estuary located near Waldport, Oregon (44°26′N, 124°3′W). The local harbor seal population in this area consisted of approximately 600 animals throughout the study period. Scat samples from this population were obtained during low tides by approaching haul-out areas on foot or by boat, and slowly moving the animals into the water. Samples were placed in individually labeled plastic bags and frozen. The number of scat samples collected during each trip varied depending on the number and location of animals hauled out, and on weather and ocean conditions.

Scats were thawed and partially dissolved in water, then rinsed through a series of nested sieves (2 mm, 1 mm, 0.71 mm). All prey hard parts (e.g., otoliths, bones) recovered were dried and placed in individually labeled jars. Prey species were identified from all prey hard parts recovered from each sample. Dried hard parts were examined under a dissecting microscope and identified by using a comparative collection of fishes from the northeast Pacific Ocean and Oregon estuaries. Otoliths and diagnostic bones were identified, counted, and the side (left or right) was noted to estimate a minimum number of individuals (MNI) represented in each sample by following the procedures described by Lance et al.[4]

Otoliths selected for aging were given individual identification numbers and stored in gelatin capsules. One sample with 65 similarly size otoliths was subsampled by randomly selecting the first 18 otoliths recovered. Before aging, otoliths were measured to the nearest mm for total length, width, and length of sulcus by using an optical micrometer. Degree of erosion (level 1 having the least amount of erosion and level 3 having the greatest) was recorded by following techniques described in Tollit et al. (1997). Reference photographs were taken of each otolith with a dissecting microscope and digital camera before age estimates were determined.

Final otolith ages were determined by using one of two techniques. First, all fish otoliths were submerged in a dish of ethanol with a black background and annuli were counted under a dissecting microscope with reflected light (i.e., surface aged). Second, fish ≥ four years were re-aged according to the method described in Pikitch and Demory (1988) (i.e., break-and-burn method). The first annulus deposited was determined to be the completion of growth for the first year following the convention for aging adult Dover sole (Chilton and Beamish, 1982). In some cases, a mark within the otolith core was counted as the initial increment because it met the identification criteria for an annual increment.

Results

Dover sole remains (bones and otoliths) were recovered from 296 of the 3370 harbor seal scat samples collected during the study period (Table 1). Dover sole otoliths were recovered from 132 of these scat samples. Eighty-nine of these otoliths (21%) were excluded from our analyses because of poor condition (erosion or breakage), extremely small size, or because they had been randomly subsampled. The majority of otoliths were moderately eroded (level 1: 16%, level 2: 64% and level 3: 20%).

Of the 339 otoliths analyzed, 98.2% were assigned an age; 71.2% (237) by surface aging and 28.8% (96) by the break-and-burn method. Six otoliths were excluded from age estimates because of extreme edge wear and erosion. Forty-nine (92.5%) of the scats with more than one otolith analyzed resulted in fish of multiple ages.

The majority (70.6%) of otoliths analyzed were from one-, two-, and three-year-old fish; the rest were from four to six year-old (25.8%) and seven to 12 year-old (3.6%) (Table 1). Of the juvenile fish otoliths recovered, the presence of one- and two-year-old fish peaked in July, and three-year-old fish were found most frequently in August. Three of the four oldest fish otoliths were recovered during the summer months, and one 10-year-old fish was recovered in May. The scat samples collected during fall (September–November) primarily included two- and three-year-old fish (72.5%).

Aging otoliths of Dover sole increased MNI in harbor seal scats by 13% (269 versus 238). In most cases the number of Dover sole increased by one fish per scat when using both age and otolith side to enumerate MNI.

Discussion

We have shown in the present study that 1) Dover sole otoliths recovered from harbor seal scats can be successfully aged, and 2) seals in the Alsea River consumed Dover sole that ranged in age from one to 12 years. Interestingly, the highest frequency of occur-

[4] Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. AFSC (Alaska Fisheries Science Center) Proc. Rep. 2001-04, 36 p. Alaska Fisheries Science Center, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Age distribution for Dover sole (*Microstomus pacificus*) consumed by harbor seals (*Phoca vitulina*), based on otoliths recovered from scats collected in the Alsea Estuary, Oregon. Total number of scats collected (n), scats with Dover sole bones and otoliths (n-Dover), and otoliths only (n-otoliths), and the number of Dover sole otoliths recovered (n) and successfully aged (n-aged) were pooled monthly over all years from 1996 through 2002.

	Scat			Otolith		Age (yr)												
Month	n	n-Dover	n-otoliths	n	n-aged	1	2	3	4	5	6	7	8	9	10	11	12	%[1]
Jan	33	0																0%
Feb	24	1	1	3	3		1	2										0.9%
Mar	103	2																0%
Apr	212	12	1	0	0													0%
May	230	22	11	12	11		6	2		2					1			3.3%
Jun	423	26	16	38	35	4	9	9	4	5	1	2		1				10.5%
Jul	347	91	40	174	118	26	32	23	18	11	6		1		1			35.4%
Aug	330	65	32	102	97	11	23	35	15	7	2		3				1	29.1%
Sep	806	54	21	65	55	1	23	17	7	4	2		1					16.5%
Oct	387	21	8	13	10	1	5	3				1						3.0%
Nov	173	2	2	20	4			2	1	1								1.2%
Dec	0																	0%
Total	3370	296	132	428	333	43	99	93	45	30	11	3	5	1	2	0	1	333

[1] Percentage of otoliths aged by month.

rence for Dover sole in our collections (ODFW[5]), and the greatest range in their age (Table 1), occurred during summer—a period when Dover sole move into shallow nearshore waters (Hagerman, 1952; Markle et al., 1992). This migration into nearshore waters brings fish into contact with an increasing population of pinniped predators.

The majority of Dover sole otoliths recovered from scats were those of fish younger than four years. In contrast, Dover sole landed in Oregon's commercial fishery between 1984 and 2004 were aged to be between three and 60 years old and the average age was 13 years (ODFW[5]). Of the 45,026 fish aged from the commercial fishery, over 50% were ages similar to those recovered from seal scat samples (four to 12 years) and had an average length of 33.4 cm. Of the fish checked, 79% were identified as mature. However, the majority (70.5%) of otoliths analyzed in our study were from one, two-, and three-year-old fish, whereas only one of the commercially caught fish was in this age range. Four- to six-year-old fish made up 0.3% of the commercially sampled fish and seven- to 12-year-olds made up the largest portion at 53.5%. This lack of younger age fish in the commercial fishery is partly due to the discarding of smaller unmarketable fish at sea. Sampson and Wood (2001) reported that from 1956 through 2000, between 5% and 14.6% of the commercial Dover sole catch at sea was discarded because of the small unmarketable size of the catch. What effect a consistent removal of older age fish and the discarding of younger fish by the commercial fishery, coupled with the take of younger age fish by an increasing number of predators could have on the population as a whole, is unknown.

Many species of marine fishes other than Dover sole contribute to important commercial fisheries in Oregon (ODFW[6]). Estimating prey age from fish otoliths recovered from seal and sea lion scats will be useful for researchers when describing impacts on long-lived marine species such as rockfish, which may be at greater risk to this long-term and increasing predation by coastal pinnipeds. Love et al. (2002) reported that rougheye rockfish (*Sebastes aleutianus*) live to at least 205 years and yelloweye rockfish (*S. ruberrimus*) to 118 years, whereas other species such as calico (*S. dalli*) and squarespot (*S. hopkinsi*) may only live for a decade or two. These older fish in some cases also have a late maturity; for example, only half of all yelloweye rockfish are mature at an age of 22 years.

As the sustainability of these species and the fisheries that target them become difficult to manage, there will be more interest in the impact of predators on these fish populations. Determining fish age has enabled biologists

[5] ODFW (Oregon Department of Fish and Wildlife). 1984–2004. Unpubl. data. [Data are on file at Oregon Department of Fish and Wildlife Newport-Marine Program office, 2040 S.E. Marine Science Drive, Newport, Oregon 97365.]

[6] ODFW (Oregon Department of Fish and Wildlife). 2000. Oregon Marine Fisheries 2000 status report, 109 p. [Available from Oregon Department of Fish and Wildlife Newport-Marine Program office, 2040 S.E. Marine Science Drive, Newport, Oregon 97365.]

to more accurately estimate appropriate fishing levels, particularly for rockfish species (Love et al., 2002). This information can also contribute to assessing the impact of pinnipeds on these species and can improve stock assessment models. Otolith age can provide information on the size of fish consumed when the age-length composition in the population or subgroup is available (Salthaug, 2003). In addition, age estimates provide information on the reproductive maturity of the prey consumed. Aging will also provide a more accurate estimate of the MNI of a particular prey species consumed than an estimate based on the maximum number of left or right otoliths of a similar size, particularly because different age fish can have otoliths of approximately the same size.

Researchers should note that the digestive process does cause erosion of otoliths and can result in underestimation of fish ages. We did not attempt to determine how otolith-based age estimates were affected by erosion, but a carefully designed captive feeding study would be able to address this issue in the future. However, because there are few other methods to determine the age distribution of fish taken by pinnipeds, this technique is useful when describing the diet of seals and sea lions.

Acknowledgments

Funding for this project was provided by the National Marine Fisheries Service, Northwest Regional Office (with the assistance of the Pacific States Marine Fisheries Commission) and the Oregon Department of Fish and Wildlife, Marine Resources Program. We thank Bryan Wright, Robin Brown, and Monique Lance for their support of this project and the editing of an earlier draft of the manuscript. We thank Patty Burke and Mark Saelens for their input and support. We extend our thanks to our field staff Aicha Ougzin, Mark Dhruv, and Jonathon Scordino. We also thank Mark Karnowski and William Miller for their help with data and revisions. Finally, we thank the two anonymous reviewers who provided comments on this manuscript.

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Habitat, age, and diet of a forage fish in southeastern Alaska: Pacific sandfish (*Trichodon trichodon*)

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The focus of our study was to provide new information on the general biology of a little known forage fish species. Objectives were to determine habitat preference, age, size, and diet of Pacific sandfish. To accomplish this, from 2001 to 2004, we captured Pacific sandfish with a beach seine in July and March and with a mid-water trawl in May near The Brothers Islands in southeastern Alaska.

Forage fish are an important part of Alaska's marine ecosystems and coastal areas. Forage fish are a critical food source for numerous groundfish, marine mammals, and seabirds (Wespestad[1]; Allen and Smith, 1988; Paul et al., 1997; Yang and Nelson, 2000; Mecklenburg et al., 2002). Little is known, however, about the life history characteristics or habitat of many forage fish species in Alaska, including Pacific sandfish (*Trichodon trichodon*; Fig. 1). Only two articles have been published on the life history characteristics of Pacific sandfish in Alaska. Paul et al. (1997) investigated size-weight-age profiles, size at maturity, and fecundity of Pacific sandfish in the northern Gulf of Alaska, and Bailey et al. (1983) examined size and diet of juvenile (<55 mm fork length [FL]) Pacific sandfish in southeastern Alaska. Some Pacific sandfish catch data are also available for the Bering Sea, Prince William Sound, and southeastern Alaska (Isakson et al., 1971; Orsi and Landingham, 1985; Allen and Smith, 1988; Brodeur and Livingston, 1988; Sturdevant et al.[2], Orsi et al., 2000). Pacific sandfish burrow into sand, usually at depths shallower than 150 m, and can reach a maximum size of about 300 mm (Marliave, 1980; Mecklenburg et al., 2002).

Pacific sandfish are commonly found in nearshore waters of the southeastern Bering Sea and Gulf of Alaska. There is no commercial fishery for Pacific sandfish in Alaska, but sailfin sandfish (*Arctoscopus japonicus*) are commercially fished and cultured in Japan and Korea (Okiyama, 1990). In particular, information is scarce on the biology and habitat of Pacific sandfish, especially for southeastern Alaska. Shoreline development and global climate change (e.g., increased water temperature and sea level) may adversely affect Pacific sandfish populations because of the relatively specialized nearshore spawning sites and one-year incubation period of this species (Marliave, 1980).

Materials and methods

Fish capture and habitat

Pacific sandfish were captured with a beach seine at The Brothers Islands in southeastern Alaska (Fig. 2). We seined 10 sites in summer (July 2001–2003) and in winter (March 2002–2004) in a variety of nearshore habitat types (Table 1). Habitats sampled included steep bedrock outcroppings, rocky bottoms with understory kelps (e.g., *Laminaria*), eelgrass (*Zostera marina*), and sand beaches. We used a 37-m variable-mesh beach seine that tapered from 5 m wide at the center to 1 m wide at the ends. Outer panels were each 10 m of 32-mm stretch mesh, intermediate panels were each 4 m of 6-mm square mesh, and the bunt was 9 m of 3.2-mm square mesh. We set the seine as a "round haul" by holding one end on the beach, backing around in a skiff with the other end to the beach about 18 m from the starting point, and pulling the seine onto shore. The seine had a lead line and a float line so that the bottom contacted the substratum and the top floated on the surface. All seine sites were sampled during daylight and within two hours of low tide (range +1.0 to −1.5 m below mean lower low water). After retrieval of the net, the entire catch was sorted, identified to species, counted, and a subsample was measured for length.

[1] Wespestad, V. G. 1987. Population dynamics of Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and other coastal pelagic fishes in the eastern Bering Sea. *In* Forage fishes of the southeastern Bering Sea; proceedings of a conference, November 1986, Anchorage, AK, p. 55–60. U.S. Dep. Interior, Minerals Management Service, OCS Study MMS 87-0017.

[2] Sturdevant, M. V., T. M. Willette, S. C. Jewett, E. Debevec, L. B. Hulbert, and A. L. J. Brase. 1999. Forage fish diet overlap, 1994–1996. APEX Project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska, 103 p. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98163C), Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Highway, Juneau, Alaska.

Manuscript submitted 16 May 2005 to the Scientific Editor's Office.
Manuscript approved for publication 1 December 2005 by the Scientific Editor.
Fish. Bull. 104:631–637 (2006).

Figure 1
Pacific sandfish (*Trichodon trichodon*) captured in southeastern Alaska.

Table 1
Habitat characteristics of sites (see Fig. 2) at The Brothers Islands in southeastern Alaska where Pacific sandfish (*Trichodon trichodon*) were captured with a beach seine from 2001 to 2004. Substrata are listed in decreasing order of abundance from left to right. For vegetation, algae were mostly *Ulva*, eelgrass was *Zostera marina*, and kelps were mostly Laminariales (e.g., *Laminaria*, *Alaria*, and *Cymathere*). PSS = practical salinity scale. Catch = number of sandfish.

						Catch	
Site	Substrate	Vegetation	Slope	Temperature (°C)	Salinity (PSS)	July 2001–03	March 2002–04
1	sand, shell	algae	gentle	4.0–9.5	32–33	6	110
2	large cobble, small cobble, gravel, shell	kelp	moderate	9.0	33	14	0
3	large cobble, sand	kelp	gentle	12.0	24	1	0
4	sand, shell, gravel, small cobble	eelgrass	gentle	12.0	33	1	0
5	small cobble, large cobble, sand, gravel	kelp	moderate	4.9–9.5	33	2	1
6	bedrock outcrop	kelp	steep	4.2–10.0	31–33	900	300
7	bedrock outcrop	kelp	steep	4.2–10.0	31–33	68	500
8	bedrock outcrop	kelp	steep	4.2	33	0	1120
9	bedrock outcrop	kelp	steep	4.0	33	0	5000
10	bedrock outcrop	kelp	steep	4.0–10.0	30–33	35	7200
					Total	1027	14,231

The number of larvae (≤30 mm) in large catches in winter was estimated visually. Water temperature and salinity (practical salinity scale; PSS) were measured at each site at a depth of 20 cm with a thermometer and a hand-held refractometer.

Pacific sandfish were also captured with a mid-water rope trawl in May 2001 in Frederick Sound, midway between the mouth of Pybus Bay and The Brothers Islands, and in May 2003 in Pybus Bay (about 12 km from The Brothers Islands) (Fig. 2). In 2001, the midwater trawl was a 164 Nordic rope trawl with 1.5-m^2 alloy doors; it was 7 m high and 17 m wide and was equipped with a 19-mm codend liner. In 2003, because a different vessel was used, the trawl was a mesh wing 25/21/64

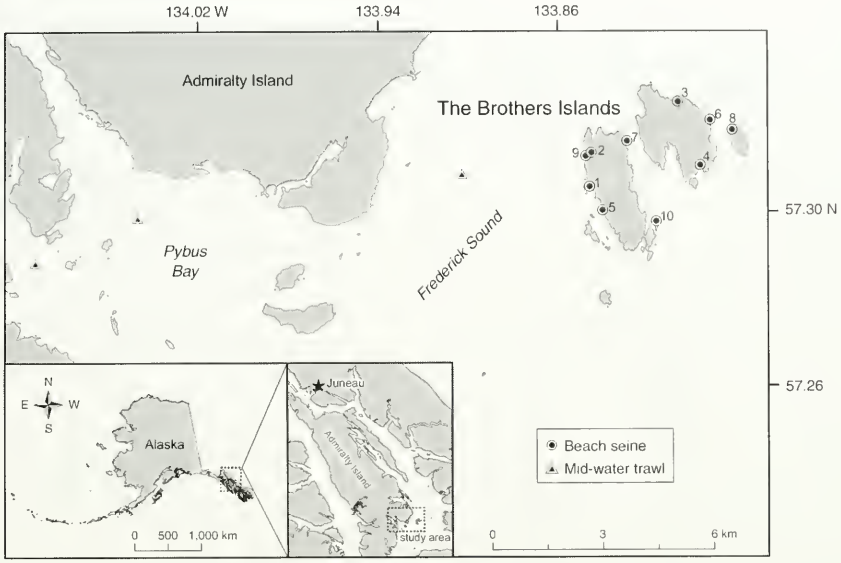

Figure 2

Location of sites (see Table 1 for habitat characteristics) sampled for Pacific sandfish (*Trichodon trichodon*) near The Brothers Islands, southeastern Alaska, 2001 to 2004. Sampling methods included beach seining and mid-water trawling.

trawl with 3.0-m^2 alloy doors; it was 11 m high and 29 m wide and was equipped with a 32-mm mesh codend liner. In Frederick Sound, water depth was about 74 m, and the trawl was fished at a depth of 14 m. In Pybus Bay, water depth was about 70 m and the trawl was fished at depths from 50 to 64 m about 400 m offshore. Water temperature and salinity were obtained from deployment of a CTD (conductivity-temperature-depth) profiler in Pybus Bay in 2003.

Age and size

A sample of Pacific sandfish was frozen and brought to the laboratory where sagittal otoliths were removed and stored in 95% ethanol. Fish used for otolith collections covered a range of sizes in the catch (Table 2). Fish were measured to the nearest mm FL, and larvae were measured to the nearest mm total length (TL). A sample of fish was individually weighed to the nearest gram. Because a sample of larvae captured with a seine and preserved (10% formalin) in 2002 was not measured until 2004, a shrinkage factor of 10.3% was applied to the lengths to adjust for storage in formalin (Marliave, 1980). The left otolith of each fish was cut into thin sections by using standard methods described in the otolith manual for microstructural examination (Secor et al., 1991). The otolith was attached to a glass slide, medial side down, with thermal resin. The surface of the otolith was then ground to the primordium with 1000-grit silicon carbide paper. Care was taken to leave the edge of the otolith intact and not to grind through the primordium in the center. The otolith was then polished with an 8000- and 12,000-grit cloth on both sides to reveal the internal microstructure. Otoliths collected in 2001 were aged separately by two biologists. When age estimates differed, otoliths were re-examined together by both readers, and an age was agreed upon. Otoliths collected in 2002 were aged by one biologist three different times. If age readings differed between any of the three readings, the otolith was re-examined and a best estimate of the age was determined. For both years, otoliths were examined without knowledge of fish size or collection date.

Diet

A sample of Pacific sandfish (>age-0) was preserved in 10% formalin and analyzed for stomach contents. Preserved fish were measured to the nearest mm FL, weighed to the nearest 0.1 g, and stomachs were excised. Stomachs were weighed before and after removal of contents to obtain an estimate of wet weight by subtraction. Contents were examined with a dissecting microscope and identified to major taxonomic groups.

Table 2

Size and age based on surface observations of annual rings on otoliths of Pacific sandfish (*Trichodon trichodon*) from nearshore waters of The Brothers Islands, and from Pybus Bay and Frederick Sound, southeastern Alaska from 2001 to 2003. Fish from Frederick Sound and Pybus Bay were captured with a mid-water trawl, whereas all other fish were captured with a beach seine. Asterisk denotes total length (mm). *n* = number of sandfish in the sample.

			Fork length (mm)			
Date	Location	*n*	Mean	Range	Mean weight (g)	Age (yr)
July 2001	The Brothers Islands	22	80	70–95	6.4	1
May 2001	Frederick Sound	1	120	—	24.0	4
May 2001	Frederick Sound	1	190	—	82.0	6
March 2002	The Brothers Islands	9	16*	14–18*	—	0
July 2002	The Brothers Islands	24	70	55–79	4.3	1
July 2002	The Brothers Islands	1	135	—	32.0	5
May 2003	Pybus Bay	1	121	—	23.5	4
May 2003	Pybus Bay	10	141	129–152	37.2	5
May 2003	Pybus Bay	7	160	156–166	58.3	6

Frequency of occurrence (% FO) was determined for each taxonomic group based on the percentage of stomachs in which that taxonomic group occurred. Percent volume (% Vol) of each taxonomic group was estimated visually and total weights per taxon were estimated by multiplying the percent volume by the total stomach weight.

Results

Fish catch and habitat

Total catch of Pacific sandfish was 15,431 fish. Most (99%) fish were captured with a seine: 1027 fish in July (total for all years) and 14,231 larvae in March (total for all years; Table 1). Total trawl catch was 173 fish; 2 fish in Frederick Sound in May 2001 and 171 fish in Pybus Bay in May 2003.

Most Pacific sandfish captured with a seine in July and March each year were found adjacent to steep bedrock outcroppings with attached kelp (Table 1). Water temperatures in summer and winter for all years were about 10°C and 4°C, and salinity ranged from 30 to 33 PSS. Larvae were captured in March at many of the same sites where juveniles were captured in July (sites 1, 9–11, 14; Table 1; Fig. 2). The few adult Pacific sandfish (>130 mm FL) captured with a seine in July 2002 and 2003 were found exclusively in low gradient, sandy habitat (site 1; Fig. 2). Most adult Pacific sandfish were captured in Pybus Bay with a trawl at least 400 m offshore of any land mass and at depths between 14 and 64 m; at the depth (50 m) most fish were captured, temperature was 6.5°C and salinity was 31.5 PSS.

Age and size

Nearly all Pacific sandfish captured with a seine in July (all years) were juveniles; only larvae were captured in March (all years). Approximately 14,000 Pacific sandfish larvae were captured in March (Table 1); mean TL was 16.2 mm (13.1 to 23.2 mm; Fig. 3). Of nine larvae aged from March 2002, all were age-0 (Table 2). Mean FL of Pacific sandfish captured with a seine in July was 86 mm (62 to 150 mm; Fig. 3). Of 47 Pacific sandfish aged from seine catches in July, 46 were age-1 (mean FL=75 mm) and one was age-5 (FL=135 mm) (Table 2).

All trawl-caught Pacific sandfish were adults or subadults. Mean FL of Pacific sandfish from trawl catches was 150 mm (120 to 190 mm; Fig. 3). The 21 fish aged from trawl catches in May (both years) were age-4, age-5, and age-6 (mean FL=121, 141, and 164 mm) (Table 2). No age-2 or age-3 fish were captured in trawls.

Diet

From analysis of 195 stomachs, we found that Pacific sandfish were both planktivorous and piscivorous. Percent weight of stomach contents for age-1 Pacific sandfish varied between years (Fig. 4). For both 2001 and 2002 combined, decapods, fish, and euphausiids accounted for about 90% of stomach content weight. Fish made up 50% of the weight in 2001, but only 7% in 2002. The other two heaviest items, decapods and euphausiids, ranged from 30% to 50% and from 17% to 25% of the weight in 2001 and 2002, respectively. Diet of adult Pacific sandfish (2003; ≥age-4) consisted of four food items and was dominated by fish and decapods (Fig. 4). Fish accounted for 75% of the weight of stomach contents for ≥age-4 fish. Frequency of occur-

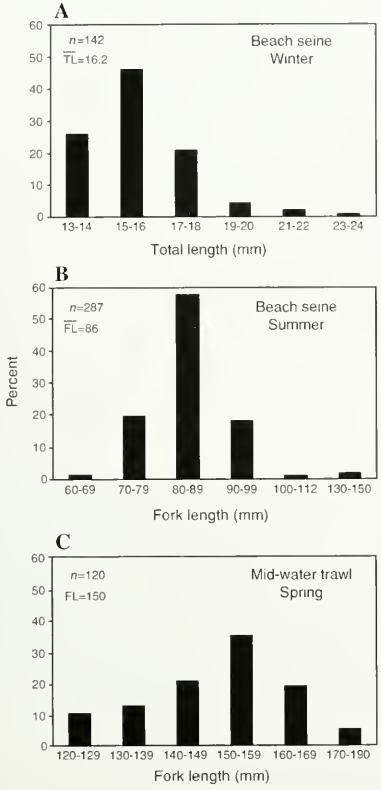

Figure 3

Length frequency of Pacific sandfish (*Trichodon trichodon*) near The Brothers Islands, southeastern Alaska. (**A**) Larvae were captured in March, 2002–2004, (**B**) juveniles and subadults were captured in July, 2001–2003, and (**C**) subadults and adults were captured in May 2001 and May 2003. Total length was measured for larvae and fork length for juveniles, subadults, and adults.

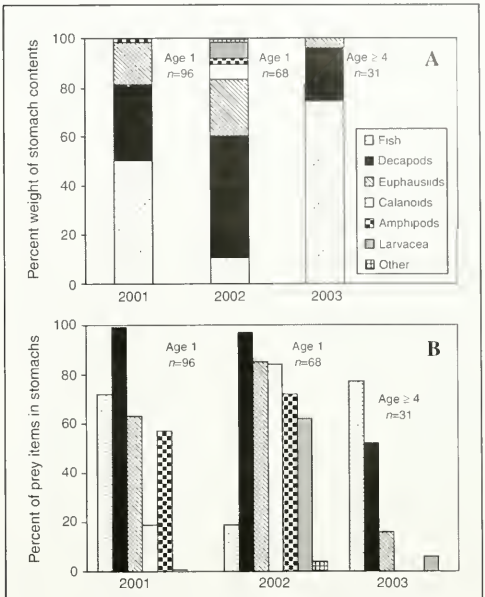

Figure 4

(**A**) Percent weight of stomach contents and (**B**) percent frequency of occurrence of prey items in stomachs of Pacific sandfish (*Trichodon trichodon*) near The Brothers Islands, southeastern Alaska. Data for 2001 and 2002 represent age-1 fish captured with a beach seine in July, and data for 2003 represent fish ≥age 4 captured with a mid-water trawl in Pybus Bay and Frederick Sound in May. See Figure 2 for site locations.

rence of food items in stomachs varied among years for age-1 Pacific sandfish (Fig. 4). Occurrence of fish in stomachs of age-1 fish ranged from 72% in 2001 to 19% in 2002, and occurrence of larvacea ranged from 62% in 2001 to 1% in 2002. Nearly all identifiable fish in juvenile stomachs were gadids. For 2001 and 2002 combined, decapod larvae occurred in about 98% of stomachs, euphausiids in 74%, and amphipods in 65%. For adults (2003; ≥age-4), fish were the most frequently occurring food item and were present in 77% of stomachs.

Discussion

Pacific sandfish larvae and juveniles use shallow, nearshore habitats, whereas most adults occupy deeper waters farther from shore. Larvae were similar in size and anatomical features to larvae (0–29 day-old) described by Marliave (1980). Thus, we estimate that the larvae we captured probably hatched between early February and early March—a hatching period similar to that reported by Clemens and Wilby (1967) for British Columbia, Canada, but 1–2 months earlier than hatching dates estimated by Bailey et al. (1983) for northern southeastern Alaska. Pacific sandfish spawn on rocky intertidal shorelines, eggs incubate for about one year, and larvae develop in shallow nearshore areas (Marliave, 1980). Because of the relative high abundance of Pacific

sandfish larvae in the shallow nearshore waters of The Brothers Islands, this area appears to be an important spawning and nursery area for Pacific sandfish. The length of time that larvae remain in shallow nearshore areas, however, appears to be limited because we captured no age-0 fish in July.

Pacific sandfish have been caught incidentally in a variety of habitats in Alaska. In southeastern Alaska, Orsi and Landingham (1985) caught Pacific sandfish in low-gradient beaches composed of sand, gravel, cobble, or a combination of these substrates, and Orsi et al. (2000) caught Pacific sandfish with a rope trawl in deeper waters. In the Aleutian Islands, Isakson et al. (1971) reported that Pacific sandfish were a prominent species in the inshore sand and gravel community. Pacific sandfish are known to burrow into soft substrates, but most of the juveniles that we captured were close to shore and adjacent to bedrock outcroppings—area and substrate similar to those observed by Bailey et al. (1983). Although Mecklenburg (2003) reported that Pacific sandfish generally burrow in sand during the day and are active at night, we observed large schools of juvenile Pacific sandfish actively feeding near the surface during the day.

Age of Pacific sandfish varied with time of capture. We captured mostly age-1 Pacific sandfish in July; mean size of age-1 fish in our study (75 mm FL) was similar to the size of age-1 fish captured in the northern Gulf of Alaska (71 mm FL; Paul et al., 1997). In spring we captured subadult and adult Pacific sandfish, and in winter we caught only larval Pacific sandfish. Notably absent in all of our catches were age-2 and age-3 fish. Paul et al. (1997) captured age-2 and age-3 Pacific sandfish by a variety of methods in the northern Gulf of Alaska. Most of their sampling, however, occurred in August and in deeper waters (29–55 m). Pacific sandfish may segregate into different habitat types depending on age and size, which may explain the absence of some age classes in our catches.

Diets consisting of crustaceans and fish have been reported for Pacific sandfish similar in size to those in our study (Paul et al., 1997; Sturdevant et al.[2]). Percent FO of fish in the diet of Pacific sandfish was 66% in the Gulf of Alaska (Paul et al., 1997), 100% in Prince William Sound (Sturdevant et al.[2]), and 56% in our study. For crustaceans, the highest % FO was for shrimp (19%) in the Gulf of Alaska (Paul et al., 1997), gammarids (46%) in Prince William Sound (Sturdevant et al.[2]), and crab larvae (83%) in our study. Near Kodiak Island, Alaska, stomach contents of 26 Pacific sandfish in July were dominated by fish (70% by number and 97% by weight; Rogers et al.[3]).

[3] Rogers, D. E., D. J. Rabin, B. J. Rogers, K. Garrison, and M. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island including ichthyoplankton, meroplankton (shellfish), zooplankton, and fish. Environmental Assessment of the Alaskan Continental Shelf, p. 529–662, vol. IV. Receptors, Fish, Littoral, Benthos. Outer Continental Shelf Environmental Assessment Program, Boulder, CO.

Percent FO of fish in Pacific sandfish stomachs was nearly four times greater in 2001 than in 2002, which probably reflects the abundance of prey. Based on seine catches at The Brothers Islands, the relative abundance of young-of-the-year (YOY) gadids, the dominant fish identified in Pacific sandfish stomachs, was over six times greater in 2001 than in 2002 (Thedinga et al., 2006). In addition, mean length of Pacific sandfish was about 5 mm longer in 2001 than in 2002, which may reflect the increased presence of fish in the diet of Pacific sandfish, or could be due to increased growth time because we sampled 10 days later in 2001 than in 2002.

Diet differed by fish size. Larger Pacific sandfish (mean FL 150 mm) ate mostly fish, whereas smaller Pacific sandfish (mean FL 86 mm) ate mostly decapods. Paul et al. (1997) also observed a change in diet based on fish size; % FO of fish in the diet of Pacific sandfish greater than 115 mm FL was 90% compared to 14% for fish less than 99 mm. Also in their study, mean % FO of non-fish food items was 5% for larger fish compared to 24% for smaller fish.

Bailey et al. (1983) reported observing juvenile Pacific sandfish in mixed schools with pink salmon (*Oncorhynchus gorbuscha*) fry, but we caught Pacific sandfish with YOY walleye pollock (*Theragra chalcogramma*), YOY Pacific cod (*Gadus macrocephalus*), YOY Pacific herring (*Clupea pallasii*), and juvenile chum salmon (*Oncorhynchus keta*). Apparently, Pacific sandfish exhibit schooling behavior as larvae and juveniles and co-occur with a variety of forage species, sometimes preying on those that are of consumable size. High predation rates of juvenile walleye pollock by Pacific sandfish have been reported for the Bering Sea and Gulf of Alaska (Guénette, 2005).

Shallow nearshore waters provide important nursery and spawning habitat for Pacific sandfish. Pacific sandfish diet varied between size classes and years which was probably dependent on abundance of YOY walleye pollock. Pacific sandfish are a nutritious forage fish with moderately high oil, protein, and caloric content (Anthony et al., 2000; Logerwell and Schaufler, 2005) and could therefore be important to some predators at certain times of the year. For example, Pacific sandfish occurred in up to 64% of Steller sea lion (*Eumetopias jubatus*) scats in the Aleutian Islands (Sinclair and Zeppelin, 2002). The dependence of Pacific sandfish upon nearshore areas for spawning, egg incubation, and larval rearing, coupled with the greater sensitivity to pollutants of early life stages than adults (Carls et al., 1999), warrant the protection of nearshore areas from shoreline development and pollutants to maintain healthy forage fish populations.

Acknowledgments

We thank D. Csepp, E. Flynn, and M. Johnson for help with fish collections and otolith removal. We also thank

K. Munk, M. Sturdevant, and M. Cook for help with age and diet analyses. D. Neff assisted with the manuscript figures. The NOAA ship *John N. Cobb* and the fishing vessel *Patriot* provided logistical support. J. Rice, A. Moles, N. Hillgruber, and K. Munk provided helpful reviews on earlier drafts of this manuscript.

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Genetic diversity of yellow grouper (*Epinephelus awoara*) determined by random amplified polymorphic DNA (RAPD) analysis

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The development of molecular techniques has enhanced our ability to identify fish species. A few molecular markers, such as mitochondrial DNA and ribosomal DNA, have been used to assist in the identification of fish species. One such technique now routinely used is the random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR; Williams et al., 1990). Genetic analysis with RAPD markers is relatively easy, fast, and efficient. RAPD analysis, however, may not be practical for identifing species that interbreed (Martinez et al., 1997). Although the major limitation of RAPD technique for identification of intraspecific specimens is its repeatability, adherence to protocol and standardized reactions can improve the method (Jones et al., 1997). This technique has been used for identification and detection of genetic diversity in various fish species (tilapia; Naish et al., 1995; striped bass; Bielawski and Pumo, 1997; grouper; Asensio et al., 2002). Most other DNA-based methods are more laborious and time consuming than RAPD, making them less suitable for large population or genetic diversity studies. Suitable loci with high reproducibility allow the identification of unequivocally distinct species (i.e., where there is large genetic differentiation between species, compared to within species; Greig et al., 2005).

Groupers (Epinephelinae: Serranidae) are among the most important and highly valued demersal species of tropical and subtropical coastal areas worldwide. In general, grouper species lack distinct morphological specializations, but color patterns and geographic location are used in the field. Some confusion exists over the names of some important Indo-Pacific grouper species (Heemstra and Randall, 1993; Sadovy, 1997) and little work has been done to establish species identities and their genetic diversity. One alternative to gathering information on these species is the use of molecular genetic markers. In the present study, RAPD analysis has been used to investigate the genetic variation in two populations of yellow grouper (*Epinephelus awoara*) from the South China Sea.

Materials and methods

Sample preparation and DNA extraction

Yellow grouper were obtained from two populations (30 individuals from Xiamen and 26 individuals from Guangdong) of the South China Sea. Muscle samples from fish were taken, placed in 95% ethanol, transported to the laboratory, and stored at −20°C until analysis. Genomic DNA was extracted according to the DNA extraction method of DeSalle et al. (1993).

Primer selection and RAPD reaction profile

Twenty primers (Table 1) were selected on the basis of presence of intense, well-distinguished, and reproducible bands for further analysis. PCRs for each population were performed in 2-μL volumes containing 100 mM Tris-HCl (pH 8.3), 500 mM KCl, 15 mM $MgCl_2$, 1 μL dNTPs, 0.4 unit rTaq polymerase and approximately 20 ng of template DNA and 1 μL of each primer. Thermocycling conditions were as follows: initial denaturation step of 95°C for 5 min., 30 cycles of 45 s at 93°C, annealing temperature of 45 s, primary extension of 72°C for 2 min., and a final extension of 72°C for 5 minutes.

Detection of amplified DNA

Electrophoresis of a 10-μL portion of the amplification reaction was performed for 45 minutes at 100 V in a 1.2 % agarose gel containing ethidium bromide (1 μg/mL) in Tris-acetate buffer (0.004 M Tris acetate, 0.001 M EDTA, pH 8.0). DNA fragments were viewed with UV transillumination and analyzed with Genescan (Gene-Geneius Bio-imaging System, Cambridge, England). Their sizes were estimated by comparison with a commercial 1-kb plus DNA ladder.

Manuscript submitted 10 August 2004 to the Scientific Editor's Office.
Manuscript approved for publication 19 December 2006 by the Scientific Editor.
Fish. Bull. 104:638–642 (2006).

Table 1

Primer details and pattern of polymorphism in two sampled populations (Xiamen and Guangdong) of *Epinephelus awoara*. SN=serial number. XM = Xiamen; GD = Guangdong.

SN	Primers	DNA sequence	No. of bands	Total no. of polymorphic loci	Polymorphic loci in the two populations		Percentage of polymorphic loci
					XM	GD	
1	S117	CACTCTCCTC	8	7	7	4	87.5
2	S465	CCCCGGTAAC	9	8	8	2	88.9
3	S513	GGACGACAAG	6	5	0	5	83.4
4	S514	CAGGATTCCC	9	5	5	4	55.6
5	S515	GGACAACGAG	7	5	5	3	71.4
6	S517	CCGTACGTAG	10	10	10	5	100.0
7	S520	ACGGCAAGGA	7	6	6	6	85.71
8	S1021	GGCATCGGCT	10	7	7	3	70.0
9	S1023	GGGTCCAAAG	8	7	2	7	87.5
10	S1026	TGCCGCACTT	8	8	8	1	100.0
11	S1036	AAGGCACGAG	10	6	6	5	60.0
12	S1037	CCTCACGTCC	7	5	5	1	71.4
13	S1040	CCTGTTCCCT	10	7	7	2	70.0
14	S1042	TCGCACAGTC	6	2	2	2	33.3
15	S1043	AGCACCTCGT	11	11	11	6	100.0
16	S1044	GAATGCGACC	7	5	5	1	71.4
17	S1045	CAGCGTTGCC	10	7	5	7	70.0
18	S1049	ACGGCACGCA	5	3	3	3	60.0
19	S1053	CAGCCGTTCC	6	4	1	4	66.7
20	S1055	GAATCCGGCA	5	3	3	3	60.0
	Total			159	121	106	74
	Percentage of polymorphic loci			76.10	66.66	46.54	

Data analysis

The presence (1) or absence (0) of RAPD products was scored for all loci based on a minimum of two replicates. Only those characters that could be reliably scored from replicate RAPD reactions were included in the analysis. Loci that failed to generate RAPD amplification products were excluded from the analysis. Probability (Fischer's exact test) was carried out to evaluate differences in homogeneity of gene frequencies across populations for each loci. Test of heterozygosity (H_T), expected heterozygosity (H_S), population differentiation (G_{ST}), and gene flow (N_m) were also conducted between two populations of *Epinephelus awoara*.

Results

Two populations of *Epinephelus awoara* were analyzed to characterize the RAPD marker for genetic variation.

Useful RAPD primers and markers for genetic variation

The first group of 20 primers (Table 1) produced a total of 159 bands, among which 121 polymorphic bands (76.10%) were observed. The 38 monomorphic bands (23.90%) could be considered, on a preliminary basis, as population diagnostic bands that allow clear differentiation among populations of *Epinephelus awoara* because they were present in all individuals analyzed. Primers S514, S1021, S1036, S1040 and S1042 generated more diagnostic bands than did other primers. The absence of these markers in related populations must, however, still be confirmed.

Primers that showed high levels of reproducibility also produced more polymorphic bands. Over five polymorphic bands (5.76) per primer were produced from 20 primers on average. All 20 primers (Table 1) yielded satisfactory amplification products for all specimens tested. Each primer produced a unique band pattern of amplified DNA. For a given primer and DNA template, a number of bands appeared intense and reproducible in all the replicates, and bands of weaker stain appeared occasionally. All primers were able to distinguish two populations of *E. awoara*, reproducing different and well-characterized banding patterns. Banding pattern variations observed with some primers were not consistent for all individuals within or between populations and therefore these variations should be attributed to intraspecific polymorphism.

High rates of RAPD polymorphism

Polymorphic rates of RAPD bands were much higher between two populations of *Epinephelus awoara*. The number of reproducible and well-resolved bands analyzed in the two populations ranged from 5 to 11. Monomorphic bands, constantly present in all individuals, varied between primers, whereas total polymorphic bands were observed 76.10% of the time for the two populations of *E. awoara*. The Xiamen population of *E. awoara* exhibited 66.66% polymorphism, whereas polymorphism was 46.54% in the Guangdong population (Table 1). RAPD fragments of fewer than 1000 base pairs were found to be more polymorphic than larger fragments.

Genetic diversity

Genetic diversity between populations was clearly illustrated in Table 2 and Table 3. The genetic diversity statistics (H_T, H_S, G_{ST}, N_m) estimated between the two populations of *Epinephelus awoara* for each primer are listed in Table 3. Nei's (1973) unbiased measures of genetic identity and genetic distance between two populations were 0.6216 and 0.4755, respectively. Within the populations, total heterozygosity varied from 0.2189 to 0.4616 and expected heterozygosity ranged between 0.1232 and 0.2920. Probability (Fisher's exact test) of homogeneity was significant at $P>0.05$ for all primers except S465, S513, S1026, S1044, and S1055.

Discussion

This study showed a considerable amount of genetic variation present in *Epinephelus awoara*. RAPD analysis generated a large number of polymorphic DNA bands (Table 1) between the populations of *E. awoara*, thus making it one of the most efficient systems for generating DNA markers. However, low levels of interspecific variation were found in RAPD profiles among strains of grouper. Therefore, it was an inefficient system for generating molecular markers for gene mapping (Liu et al., 1999).

Several authors (Welsh and McClelland, 1990; Bardakci and Skibinski, 1994; Naish et al., 1995) have demonstrated that the RAPD PCR method is a powerful tool for the assessment of genetic markers that are capable of discriminating between species or subspecies in a wide range of organisms, including fishes. This capacity was confirmed by the results of the present study because, for all screened primers, different RAPD banding patterns were observed between the two populations (Table 1). A limitation arising with the application of the RAPD technique is the homology between comigrating bands produced by the same primer in different individuals (Hadrys et al., 1992). Nevertheless, in the present study, homology constitutes a valid assumption because all individuals belong to the same species.

Despite the fact that no specific markers were found to identify *Epinephelus awoara* species, data analysis of the observed and effective number of alleles revealed a degree of divergence (Table 2). The Nei (1973) gene diversity was also illustrated in Table 2. The two populations of *E. awoara* (Table 3) showed high level of genetic variation (i.e., Shannon's information index; Shannon-Weaver, 1949, average genetic index [H_{POP}] and genetic diversity index between populations [H_{SP}]). Similarly a high level of genetic variation and genetic distance (0.617–0.949) was observed in dinoflagellates (Baillie et al., 2000). This finding supports a high genetic distance for *E. awoara* (0.4755) in the present study. This may be due to the selection pressure of pollutants (Nadig et al., 1998) or to overexploitation of groupers in the South China Sea.

Total heterozygosity (H_T) values ranged from 0.2189 to 0.4616, expected heterozygosity (H_S) from 0.1232 to 0.3157, and an estimate of gene flow (N_m) from 0.3714 to 4.1722. The proportion of total genetic variation within species due to population differentiation (G_{ST}) ranged from 0.1070 to 0.5344 (Table 3). Carvalho et al. (1991) observed a very high differentiation (G_{ST}=0.648) in the guppy (*Poecilia reticulata*) in northern Trinidad. Similarly, Ward et al. (1994) also observed high G_{ST} values (>0.2000). In any case, the divergence in G_{ST} values indicates that, on average, marine subpopulations exchange between one and two orders of magnitude more migrants per generation. Genetic divergence between areas originates when populations are formed or through the restriction of gene flow (Lage et al., 2004). Higher H_S in marine fish is at least consistent with these fish having, on average, larger population sizes. Homogeneity of gene frequencies was found to be significant ($P>0.05$) across populations of *Epinephelus awoara* (Fig. 1) for most of the primers except S465, S513, S1026, S1044,and S1055 ($P>0.001$).

The factor that could influence the genetic variation of the grouper population geographically is the movement of adults, which can be extensive and cover considerable distances (Harding et al., 1997). The otherwise shelter-habituated adults travel long distances necessary to populate remote oceanic islands. The Bermuda fauna include more than 75% of the known west Indian groupers even though Bermuda lies more than 800 miles from other coral reefs. Such distributional patterns are best explained as the result of passive transport of larvae by oceanic currents. Similar patterns are also expected in the South China Sea. Adult movement of marine fish is relatively unfettered by physical barriers. In addition to gene flow through adult migration, marine fish frequently have a planktonic larval stage of several months duration, which can be expected to further enhance gene flow.

Estimation of genetic diversity of *Epinephelus awoara* by RAPD analysis (i.e., by using the mean of observed number of alleles [*Na*], effective number of alleles [*Ne*] and Nei's gene diversity [*H*]) was found to be 1.6563, 1.4169, and 0.2915, respectively for Xiamen populations, whereas they were 1.4824, 1.2713, 0.2167, respectively for Guangdong populations. Our results provide evidence for a loss (10.5%, 11.3%, and 25.7%, respec-

Table 2

Genetic variation in two sampled populations (Xiamen and Guangdong) of *Epinephelus awoara*. Na = Observed number of alleles; *Ne* = Effective number of alleles; *H* = Nei's (1973) gene diversity; *Ho* (I) = observed heterozygosity (Shannon's information index).

	Na		*Ne*		*H*		*Ho* (I)	
Loci	Xiamen	Guangdong	Xiamen	Guangdong	Xiamen	Guangdong	Xiamen	Guangdong
S117	1.8750	1.5000	1.5318	1.2272	0.3145	0.1449	0.4675	0.2254
S465	1.8889	1.1111	1.6659	1.0927	0.3673	0.0505	0.5324	0.0719
S513	1.0000	1.8333	1.0000	1.5851	0.0000	0.3298	0.0000	0.4819
S514	1.5556	1.4444	1.3886	1.1905	0.2231	0.1310	0.3269	0.2074
S515	1.7142	1.4285	1.2984	1.1368	0.1924	0.1019	0.3076	0.1565
S517	2.0000	1.5000	1.6602	1.2678	0.3886	1.1696	0.5808	0.2593
S520	1.7142	1.8571	1.5315	1.5871	0.2877	0.3580	0.4162	0.5048
S1021	1.8000	1.3000	1.3246	1.1497	0.1959	0.0946	0.3077	0.1463
S1023	1.2500	1.8750	1.1780	1.4712	0.1004	0.3229	0.1469	0.4806
S1026	2.0000	1.1250	1.6661	1.0575	0.3859	0.0394	0.5691	0.0618
S1036	1.7000	1.4000	1.3534	1.3771	0.3038	0.1940	0.2334	0.2712
S1037	1.7142	1.1428	1.4307	1.0318	0.2254	0.0260	0.3769	0.1039
S1040	1.7000	1.2000	1.5307	1.0605	0.3011	0.0464	0.4348	0.0786
S1042	1.3333	1.3333	1.2429	1.1814	0.1358	0.1107	0.1945	0.1689
S1043	2.0000	1.4545	1.7466	1.1649	0.4081	0.1044	0.5911	0.1694
S1044	1.7142	1.1428	1.4483	1.0057	0.2689	0.0054	0.3997	0.0136
S1045	1.5000	1.8000	1.4107	1.5349	0.2189	0.3146	0.3126	0.4642
S1049	1.6000	1.6000	1.5417	1.3333	0.2839	0.2124	0.3994	0.3228
S1053	1.6666	2.0000	1.1519	1.4657	0.0795	0.3059	0.1116	0.4780
S1055	1.4000	1.6000	1.2359	1.5058	1.1478	0.2722	0.2223	0.3871
Mean	1.6563	1.4824	1.4169	1.2713	0.2915	0.2167	0.3466	0.2527

tively for *Na*, *Ne*, and *H*) of genetic diversity; this loss may be due to high fishing pressure of the grouper population in Guangdong.

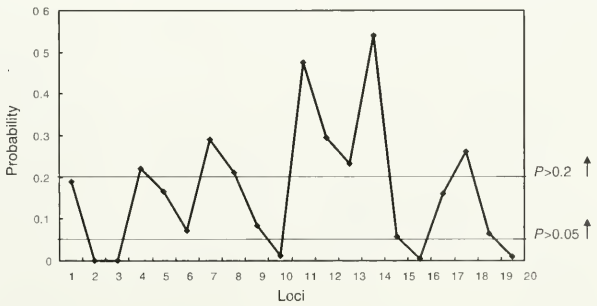

Figure 1

Probabilities ($P>0.05$) that show the significance of homogeneity of gene frequencies across populations of yellow grouper (*Epinephelus awoara*). Arrows show the range of probability.

Conclusion

These results indicate that commercial fishing may result not only in selective genetic changes in exploited stocks but also in reduced genetic diversity due to genetic drift. The loss of genetic diversity may be particularly pronounced during the initial stages of exploitation, and investigations into the advanced stages of exploitation may be less likely to detect significant changes in allelic diversity. This loss can also be tested for other commercially exploited species of grouper in genetic and demographic context. In the present study, the RAPD method proved useful and technically convenient for the study of genetic diversity of yellow grouper (*Epinephelus awoara*); therefore, it can also be applied to other species of grouper and enable the analysis of many samples in a short time. The present work also indicates that molecular markers used

in present study are a practical approach for studies of genetic diversity

Acknowledgments

This work was supported by the Project NSFC 4030602, NFC 40576064 and 2002N009 from The Science & Technology Department of Fujian Province. The first author is grateful to the Chinese Government Scholarship Council and to the Ministry of Human Resource and Development, Govt. of India, for providing financial assistance for this study.

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Improving the precision of otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) with preparation methods adapted for fragile sagittae

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Otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) have low precision, and there is general uncertainty about their accuracy in older fish (Anon.[1]; Alpoim et al.[2]). Low precision can result from inadequate training of age readers, poor aging criteria, or peculiarities of the structure being aged (Kimura and Lyons, 1991). The latter is the primary cause of low precision with Greenland halibut, and it confounds attempts to improve the former two. Sagittae of Greenland halibut are irregular in shape and exhibit marked bilateral asymmetry (Fig. 1). Much of this irregularity is due to finger-like projections, which begin as small, marginal tubercles in 4- to 6-year-old fish, and can develop into convoluted, fragile structures in older fish. The variable deposition rate of aragonite and protein that produces these structures makes interpretation of growth patterns difficult and results in age estimates that vary depending on which region of the otolith is examined.

The amphiboreal distribution of Greenland halibut has led to their exploitation by the industrial fisheries of more than ten nations in the North Atlantic and North Pacific Oceans and by several aboriginal fisheries in the near shore regions of Greenland and northern Canada (Alton et al., 1988; Witherell[3]; Anon.[4]; Treble[5]). Age determination (aging) and age structure analysis have been undertaken primarily for North Atlantic and Barents Sea stocks. Methods vary between laboratories but the majority of aging is accomplished by examining the surface patterns of whole sagittae. For the purposes of this note, "surface" (or "surface aging") will refer to the surface pattern of the whole sagitta. Generally, only the left (i.e., blind side of fish) sagitta is aged because it has a more centric nucleus, resulting in more evenly spaced annuli (Lear and Pitt, 1975; Bowering, 1978, 1982; Haug and Gulliksen, 1982; Anon.[1]; Bowering and Nedreaas, 2001; Alpoim et al.[2]). Attempts to improve the resolution of growth patterns have included baking both sagittae, clearing them with oil, grinding the distal surface of the left sagitta, and breaking and burning the left sagitta (Anon.[1]; Kuznetsova et al., 2001; Alpoim et al.[2]). To date these processes have had equivocal effects on the precision of age estimates. International exchanges of Greenland halibut otoliths have yielded mixed results; reported between-reader agreement (±0 year) has ranged from 1% to 69% (Anon.[1]) and from 37% to 51% (CVs ranging from 5.81% to 9.58%) (Alpoim et al.[2]). Despite these exchanges, concern about precision still exists and a consensus on preferred aging methods for Greenland halibut has not been reached.

The Alaska Fisheries Science Center (AFSC) has collected Greenland halibut otoliths from the Bering Sea and Aleutian Islands for over 20 years, but little aging was attempted prior to 2003. Initial examination of the otoliths left AFSC age readers

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Manuscript submitted 12 May 2005 to the Scientific Editor's Office.

Manuscript approved for publication 6 January 2006 by the Scientific Editor.

Fish. Bull. 104:643–648 (2006).

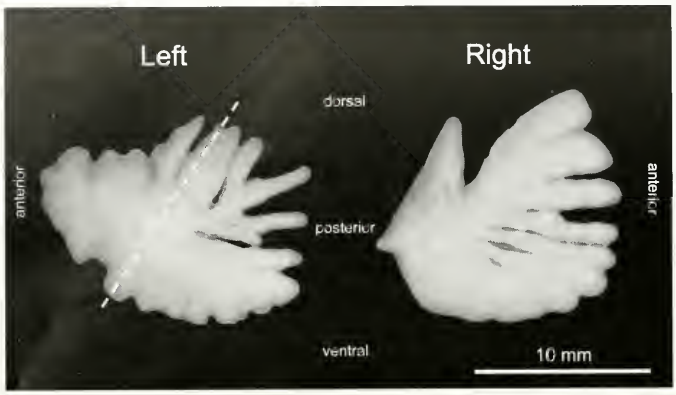

Figure 1

Micrograph of sagittae from a 92-cm Greenland halibut (*Reinhardtius hippoglossoides*). View is of the distal surface. Dashed line indicates the plane of the cross section used in this study.

with a general lack of confidence in surface age estimates. This uncertainty, coupled with the observation that otoliths of larger, presumably older, fish tend to grow in thickness rather than in sagittal diameter, led to pilot work for processing and production (large-scale) aging of Greenland halibut sagittae. Various methods reported in the literature and several new techniques were explored. This pilot work converged on a method that involved cutting the left sagitta in the transverse plane and staining the two restulting cross sections. This method is similar to the break-and-burn method (Chilton and Beamish, 1982) but is more amenable to fragile Greenland halibut sagittae. The goal of the present study was to determine whether the precision of Greenland halibut age estimates could be improved by examining the stained cross sections of their sagittae rather than the surfaces of the whole sagittae, and to determine whether there was a significant difference in age estimates made with each of the two methods.

Materials and methods

Otoliths were collected from Greenland halibut in July 1998 and June–August 1994 as part of the AFSC Bering Sea and Aleutian Islands trawl surveys. Sagittae were removed at sea and stored in a glycerol-thymol solution until the time of our study. Fish length (TL) was measured to the nearest centimeter for each specimen.

Surface aging was accomplished by submerging sagittae in water over a black background and counting probable annuli (i.e., translucent zones) with a dissecting microscope (6–25×) with reflected light. Probable annuli were counted along several vectors on both sides of the right and left sagittae. A count that was repeatable, with highest reader confidence, was adopted as the surface age estimate.

The left sagitta (i.e., on blind side of fish) was embedded in clear polyester resin and cut into two pieces with a low-speed saw. The cut was made slightly obliquely to the transverse plane and was adjusted for each otolith to ensure that the saw blade bisected the nucleus, passed through a thick section of the perisulcular region (i.e., a portion with a large mediolateral dimension), and extended out the center of a prominent dorsal finger (Fig. 1). The two exposed cross sections were then polished with 800-grit wet-dry sandpaper on a lapidary wheel to remove saw marks.

Staining techniques were adapted from Richter and McDermott (1990). Polyester blocks containing cut otoliths were submerged in a solution of 1% Aniline Blue WS (no. B362-03, Mallinckrodt Baker Inc., Phillipsburg, NJ) in 1% acetic acid. Staining times varied from 10 to 15 minutes initially and were consolidated to 13 minutes as the experiment progressed. Stain solution temperature was maintained between 20° and 23°C. Upon removal from the stain, otoliths were rinsed with fresh water and wiped clean to ensure that residual acid and stain were removed. The two cross sections were covered with mineral oil to eliminate glare, and were examined under a dissecting microscope at 12× to 50× magnification with reflected light. Blue stained translucent zones (Fig. 2) were counted, and this number was adopted as the cross-section age estimate.

Three trials were conducted to examine the possible benefits of cutting and staining Greenland halibut sagit-

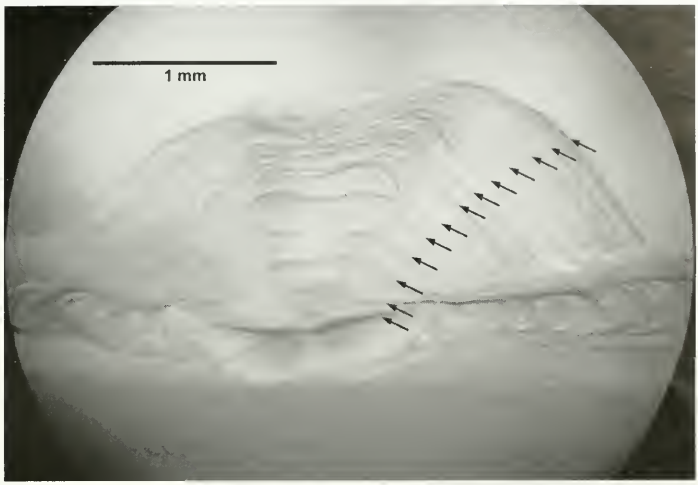

Figure 2

Stained cross section of the left sagitta from an 84-cm Greenland halibut (*Reinhardtius hippoglossoides*). Arrows point to presumed annual marks in the perisulcular tuberosity where annuli were most readily resolved. Fish age was estimated at 13 years.

tae. In trial 1, a training trial, sagittae of 93 Greenland halibut were examined to compare precision between the two aging methods and to calibrate age readers with respect to the first few annuli on the stained cross sections. This sample included fish that ranged from 12 to 84 cm TL, but it was dominated by smaller fish (mean TL=40 cm, median=31 cm). Two readers independently aged sagittal surfaces and stained cross sections. Surface aging necessarily preceded cutting and staining, but no consultation occurred between readers until the end of the trial. Readers were aware of fish length during aging. At the end of trial 1 the independently determined age estimates were compared and readers re-examined otoliths that had resulted in age discrepancies.

In trial 2, 226 otolith pairs were examined. This sample contained sagittae from many larger specimens (mean TL=75 cm, median=72 cm, and range=57 to 98 cm). Ages were determined in the same manner as in trial 1. However, after surface aging, readers re-examined discrepancies together and assigned, by mutual agreement, a definitive surface age to each sagitta prior to cutting and staining. Similarly, the cross sections were aged independently and then assigned a definitive cross-section age by mutual agreement. This process is similar to that used for production aging of other species at the AFSC (Kimura and Lyons, 1991) and allowed not only a comparison of precision between methods but also a comparison of the final age estimates that resulted from the two methods. In trial 3, sagittae were examined from 76 Greenland halibut with a size range of 12 to 63 cm TL (mean=37 cm, median=39 cm). This trial was conducted in the same manner as trial 2, with the exception that fish length was not provided to the readers. We felt that criticism could arise if length data were known because of the potential for reader bias when aging small fish that fall into distinct size classes.

Two age readers performed each trial. Reader 1 was relatively inexperienced with six months of experience aging larval otoliths and one month of experience aging adult otoliths. Reader 2 had 14 years of experience aging several species, including other Bering Sea flatfishes. Neither reader had previously aged Greenland halibut.

Between-reader agreement and coefficient of variation (CV) were calculated for each aging method from each trial. CV was used as the measure of precision (Chang, 1982). Percent agreement is not a good measure of precision because it is highly dependent on the age structure of the sample. Bowker's test of symmetry (Hoenig et al., 1995) was used to assess between-reader bias. Definitive ages from trials 2 and 3 were compared by using a two-tailed matched pairs t-test (Snedecor and Cochran, 1967). Von Bertalanffy growth parameters were estimated from surface and cross-section ages combined from trials 2 and 3. An F-test based on the residuals of nonlinear least-squares fit was used to test for difference between the resulting models (Quinn and Deriso, 1999).

Results

Stained cross sections improved the precision of Greenland halibut age estimates for the larger, presumably older, specimens in trial 2 but did not improve precision of estimates for specimens in trials 1 and 3. Percent CVs were 11.33, 16.31, and 8.11 for surface ages and 19.68, 9.64, and 9.96 for cross-section ages from trials 1, 2, and 3, respectively (Table 1). A similar pattern occurred in the symmetry of age estimates. Bowker's test of symmetry indicated that surface age estimates in trial 2 were significantly biased between age readers ($P<0.0342$) and that cross-section estimates were not ($P<0.2159$), whereas in trials 1 and 3 significant bias occurred in the cross-section estimates ($P<0.0001$ and $P<0.0012$, respectively) (Table 1).

These equivocal results were primarily caused by difficulty interpreting the second annuli on cross sections. Reader 1 tended to count a small diameter mark close to the nucleus as the second year whereas reader 2 considered it a check. A *post hoc* correction of this bias in trial 1 (i.e., adding 1 year to each of reader-2's cross-section estimates) yielded better precision (CV=7.68) and no significant bias ($P<0.2440$) (Table 1). This problem in interpretation occurred in all trials but the resulting bias was most noticeable in trials 1 and 3 where fish age estimates were younger.

Definitive cross-section ages were significantly greater (older) than definitive surface ages for trial 2 ($t=17.32$, df = 225, $P<0.0001$). Mean cross-section age was 17.1 years and had a range from 9 to 36 years, whereas mean surface age was 12.4 years and had a range from 7 to 28 years (Fig. 3A). Differences between definitive cross-section ages and definitive surface ages in trial 3 were not significant ($t=1.74$, df=74, $P<0.0858$). Mean stained age was 4.29 years and had a range from 1 to 7 years, and mean surface age was 4.15 years and had a range from 1 to 8 years (Fig. 3B). Von Bertalanffy growth parameters calculated from the definitive surface ages (trial 2 and 3 combined) were $L_\infty=103.7$, $K=0.104$, and $t_0=-0.333$. Parameters from definitive cross-section ages were $L_\infty=86.2$, $K=0.125$, and $t_0=-0.233$. The models varied significantly from each other ($F=40.58$, $P<0.0001$) (Fig. 4).

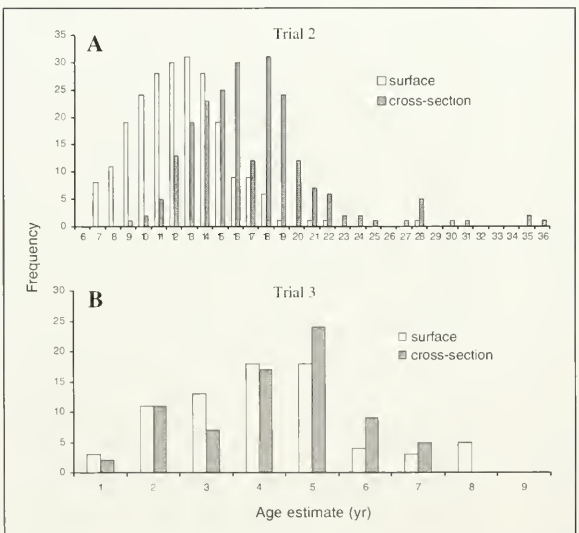

Figure 3

Age frequencies for age estimates from sagittal surfaces and from sagittal cross sections of Greenland halibut (*Reinhardtius hippoglossoides*) in trial 2 (**A**) and trial 3 (**B**) of this study.

Discussion

In larger Greenland halibut (i.e., in trial 2), the precision of age estimates can be improved by aging stained cross sections of sagittae rather than aging sagittal surfaces (Table 1). The sagittae of larger, older Greenland halibut are very difficult to interpret from the surface. Marginal growth increments are very small and are interrupted by the fingerlike projections on the otoliths. Age readers in our study were more confident in the age estimates they made from stained cross sections. The clearest annuli were encountered in the perisulcular region of left sagittae. This region appears to grow more consistently than other areas of the otolith. Staining allowed resolution of very narrow increments in this region that were not visible on the surface of sagittae.

Precision did not increase in trials 1 and 3 (Table 1) because these trials contained many smaller specimens. The benefits of cross-sectioning and staining are not as great in otoliths that are still growing rapidly in sagittal diameter. The magnitude of the difference in age estimates from whole surfaces and stained cross sections did not exceed 1 year in fish less than 46 cm and did not exceed 2 years in fish less than 57 cm. A second confounding factor was interpretation of the second annuli in cross sections. This consistent one-year bias between readers outweighed any improvements that may have resulted from cross-sectioning otoliths in smaller specimens. We feel that more interreader calibration and validation of cross-sectioned annuli by the Peterson method (Ricker, 1975) can resolve this problem.

The increase in precision in trial 2 was accompanied by age estimates that were significantly greater (older) (Fig. 3A). In 24 cases, the cross-section estimate was 10 or more years greater than the surface age estimate, and in two cases the cross-section estimate was 22 years greater. The mean

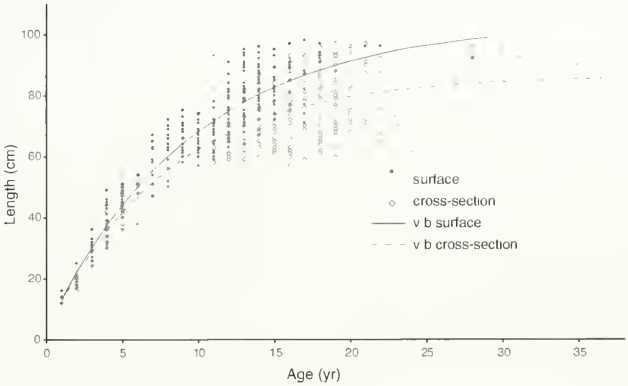

Figure 4

A comparison of plots of length at age for surface ages and cross-section ages of Greenland halibut (*Reinhardtius hippoglossoides*). Von Bertalanffy (vb) growth curve fits for surface aging (solid line) and cross-section aging (dashed line) are shown.

Table 1

Precision of age estimates made from the surfaces and cross-sections of Greenland halibut (*Reinhardtius hippoglossoides*) sagittae. Data from three trials with mean fish length and collection location indicated. BS = Bering Sea, AI = Aleutian Islands.

		Collection year, location	Mean fish length (cm)		Percent CV[1]	Between reader % agreement			Bowker's test of symmetry[2]		
	n			Ageing method		±0 yr	±1 yr	±2 yr	χ^2	df	*P*<
Trial 1	93	1998, BS	40	surface	11.33	44.1	81.7	90.3	30.4	22	0.1091
				cross-section	19.68	20.4	66.7	81.7	74.0	28	0.0001
				cross-section corrected[3]	7.68	53.8	81.7	93.5	27.3	23	0.2440
Trial 2	226	1994, AI	75	surface	16.31	16.8	42.0	58.4	94.2	71	0.0342
				cross-section	9.46	16.3	44.3	68.1	76.9	68	0.2159
Trial 3	75	1994, AI	37	surface	8.11	65.3	89.3	93.3	19.5	11	0.0532
				cross-section	9.96	49.3	90.7	98.7	32.3	12	0.0012

[1] Percent CV = coefficient of variation × 100; CV calculated following Chang (1982).

[2] $P<0.05$ from Bowker's test indicates asymmetry of discrepancies between readers (i.e., reader bias).

[3] Corrected cross-section statistics from trial 1 are the result of a *post hoc* adjustment of reader 2's ages (see text).

age estimate increased by 4.7 years for 226 fish with mean length of 75 cm. The oldest surface age estimate was 28 years and the oldest cross-section estimate was 36 years (Fig. 3A). Maximum ages of Greenland halibut reported in the literature rarely exceed 20 years (Alton et al., 1988). These older ages result in smaller size-at-age and have the effect of decreasing estimates of von Bertalanffy's L_∞ (Fig. 4).

The older cross-section age estimates for Greenland halibut are consistent with natural mortality estimated by the gonadosomatic index method (M=0.112; Cooper et al., in press). Our maximum cross-sectioned age of 36 years indicates M = 0.115, as opposed to an M = 0.149 as indicated by the maximum surface age of 28 years (Hoenig, 1983). Current natural mortality parameters used in management are 0.18 in the Bering Sea and

Aleutian Islands (Ianelli et al.[6]) and 0.20 in the North Atlantic (Darby et al.[7]). These values are more consistent with surface age estimates.

We feel that age estimates made from stained cross sections are an improvement over surface age estimates for Greenland halibut. However, validation of the age estimates produced by these methods is necessary. Given the large discrepancies that we encountered in some specimens (10 to 20 years) these ages can be roughly tested with tag-recovery or radiometric methods.

The methods used in the present study may have application in other hard-to-age species. They are a practical alternative to serial thin sections because the preparation time is shorter and allows the method to be adapted for production aging. The embedding process also preserves the structure of fragile otoliths which can be damaged during the cutting and break-and-burn processes.

Aknowledgments

This publication was funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement no. NA17RJ1232, contribution no. 1143. The project was administered by Don Gunderson. We thank Mark Blaisdell, Lyle Britt, Charles Hutchinson, Chris Johnston, Craig Kastelle, and Jon Short for technical advice on this project. Dan Cooper and Margaret Treble provided valuable Greenland halibut life history information and advice on the manuscript.

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This statement is required by the Act of August 12, 1970, Section 3685, Title 39, U.S. Code, showing ownership, management, and circulation of the *Fishery Bulletin*, publication number 366-370, and was filed on 31 August, 2006. The *Bulletin* is published quarterly (four issues annually) with an annual subscription price of $55.00 (sold by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402). The complete mailing address of the office of publication is NMFS Scientific Publications Office, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115. The complete mailing address of the headquarters of the publishing agency is National Marine Fisheries Service, NOAA, Department of Commerce, 1335 East-West Highway, Silver Spring, MD 20910. The name of the publisher is Willis Hobart and the managing editor is Sharyn Matriotti; their mailing address is: NMFS Scientific Publications Office, 7600 Sand Point Way NE, BIN 15700, Seattle, WA 98115. The owner is the U.S. Department of Commerce, 14th St. N.W., Washington, DC 20230; there are no bondholders, mortgages, or other security holders. The purpose, function, and nonprofit status of the organization (agency) and the exempt status for Federal income tax purposes has not changed during the preceding 12 months. The extent and nature of circulation is as follows: total number of copies (A) (average number of copies of each issue during the preceding 12 months) was 1107 and the actual number of copies of the single issue published nearest to the filing dates was 1101. Paid circulation (B) is handled by the U.S. Government Printing Office, Washington, DC 20402, and the total number printed for sales (mail subscriptions and individual sales) was 225 for the average number of copies each issue during the preceding 12 months and 225 the actual number of copies of the single issue published nearest to the filing date (C). Free distribution (D) by mail; samples, complimentary and other free copies (average number of copies each issue during the preceding 12 months) was 817 and the actual number of copies of the single issue published nearest to the filing date was 811. Free distribution outside the mail (E) by carriers or other means was 0 for both average number of copies and actual number of copies. Total free distribution (F) was 0 for both average number of copies and actual number of copies of the single issue published nearest the filing date. The total distribution (G: sum of D and B) (average number of copies each issue during the preceding 12 months) was 1042 and the actual number of copies of the single issue published nearest to the filing date was 1036. There were 65 copies (avg. annual) not distributed (H). The total (I: sum of G and H) is equal to the net press run figures shown in Item A: 1107 and 1101 copies, respectively. I certify that the statements made by me above are correct and complete: (Signed) Willis Hobart, Publisher.